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INCREASE OF LEARNING CAPABILITY WITH INCREASE OF BRAIN-SIZE

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Many lines of descent, especially in mammals, show a successive increase of body size (Cope's rule) and hence also an increase of *absolute* brain size. But normally the *relative* brain size is less in larger species. This latter rule, already discovered by A. von Haller in 1762, may be explained by the fact that most innervated parts of the body, especially the outer and inner surfaces, grow by the square, but the central nervous systems by the cube. Therefore the brain of larger animals may be relatively smaller without diminishing its central nervous functions. Nature "tries," so to say, to keep the nervous functions practically alike. But apparently with increase of body size the persistence of a totally balanced structural brain type becomes difficult, because the relative growth ratios of practically all brain regions are different and will hence shift the proportions of the brain.

Moreover in long lines of descent we often find Haller's rule superimposed upon another rule indicating that there exists also a special, progressive evolution of the brain, by which the relative brain size is sometimes increased. This rule of progression especially applies to the highest nervous centers, in insects chiefly to the Corpora pedunculata, in higher vertebrates particularly to the forebrain (cf. for example, the skull casts of the horse line: Edinger, 1948). The progression is not only evident from the quantity of neurons and of their arrangement, but also from their improved properties. In most cases the neurons became more densely arranged in the course of evolution and form more special centers, and the cells partly develop a richer ramification. The sensory neurons generally remain very small, but the number of them is considerably enlarged. The detailed perception of complex stimuli brought about by physiological processes of the sense organs can thus be separately represented also in the central nervous systems. Thus it became easier to react specifically to small parts of a complex stimulus pattern. On the other hand a more detailed formation of

engrams became possible, and the perception and retaining of a Gestalt became easier. Probably these advantages proved decisive in the parallel development of very numerous, particularly small sensory neurons in the three most progressive types of brain, in cephalopods, in insects and in vertebrates. On the contrary motor neurons often became especially large, because of the motor reactions to complexes of different stimuli required to comprise many excitations in the sense of a resultant and to conduct the motor excitation quickly to the effectors.

But now as absolute body size and therefore a certain brain size connected with it is an important selective (mostly not a genetical) unit, we will take no account of the share of Cope's and Haller's rule and the rule of progression in the single cases, and we will only examine the importance of different absolute brain size in phylogeny. When we compare large and small brains of related animals of different body size as a model of a real line of descent following Cope's rule we can note strong histological differences at first, because the single regions show different growth ratios, being positively or negatively allometrical. During the last years we have been working on these problems in more detail in our Zoological Institut in Münster. As I already have summarized a large part of the results (Rensch, 1954 a, b), I may restrict myself to the most important and to the more recent results.

INVERTEBRATES

In different orders of insects H. Goossen (1949) showed that most large species have more complicated Corpora pedunculata than related smaller species, that is the Corpora pedunculata show more or deeper foldings in the frontal side of their neuropil (which in some respect are parallel to the foldings of the mammalian cortex). The number of globuli-cells is always much larger in larger species, for example, in a maximum section (10μ thick) of the Corpora pedunculata this number was 615 in the large water-beetle *Dytiscus marginalis* (length 27 mm), but only 188 in the small water-beetle *Ilybius fenestralis* (length 12 mm). Probably this difference is the result of a chiefly positive allometrical growth of the Corpora pedunculata, being effective in holometabolic insects mostly at the end of the larval development (Jonescu, 1909). In hemimetabolic insects the situation is different. In our Laboratory R. Neder (unpublished) compared the postnatal development of the brain of three species of Blattidae. He showed that in *Periplaneta americana* a period of positive allometry of the Corpora pedunculata is found in the first and second larval stages, but that this growth-gradient later turns into a weaker negative allometry. Corresponding to this fact the giant cockroach Macropanesthia from Australia shows a decrease of the relative size of the Corpora pedunculata compared with smaller species (Day, 1950).

Now, the relatively larger size of this progressive brain region, serving only for connecting nervous conductions, also affects the behavior. The larger European Vespidae and Apidae (Vespa, Polistes, Apis, Bombus, etc.)

generally have more complicated social instincts. All small species of both families, in which the Corpora pedunculata are simpler, show no social life (Symmorphus, Ancristocerus, Lionotus; Andrena, Halictus, etc.). [The brain-structure of some rather small social Apidae and Vespidae of the tropics ought to be examined.] Among ants the small Ponerinae have simpler social instincts than the larger Camponotinae, and the smallest ant-species *Monomorium salomonis* (length 1.8–2.5 mm) shows only poor social instincts. Among the Scarabaeidae the large species like Scarabaeus, Copris, Geotrupes show complicated instincts in the care of their eggs (when constructing breeding-pills from dung, subterranean canals, breeding chambers), whereas the many small species of the related genus Aphodius have not such instincts, simply depositing their eggs in dung. The same holds good for the Silphidae, in which the large species of Necrophorus show very complicated breeding instincts (by digging in the carcass, feeding of the begging young larvae), whereas the small species of the related genus Catops (only 3mm long) show nothing like this.

Whether the learning capability of insects depends upon the absolute brain size or not, cannot yet be decided. Some years ago I performed some training experiments and at first I had some positive results, (Rensch, 1949), showing at least longer retention in the larger species. But the sources of errors still were too large and the experiments must be repeated.

VERTEBRATES

But in vertebrates the relations between absolute brain size, histological brain structure and learning capability are rather striking. These relations are of interest, because they contribute to a selective explanation of Cope's rule of general phyletic increase of body size. An analysis of these relations required: 1) histological studies on the growth ratio of the single regions and areas of the brain during ontogeny; 2) corresponding histological inquiries upon the differences of adult brains in related species of different body size (as a model of the real lines of descent); 3) corresponding inquiries upon sense organs, and 4) upon hormone glands; 5) comparative inquiries upon instincts, capabilities of learning, retaining and generalizing in related animals of different body size. Up to the present we could only tackle a part of such a large program, but we already have some more general results.

First Harde (1949) showed that in the forebrain of white mice the single regions and areas show specific growth ratios. Thus the cytoarchitectonic proportions differ at each ontogenetic stage, and sometimes also a reversal of the direction of allometry may occur. For example, the holocortex 5-stratificatus grows mostly with positive allometry (in relation to the whole cortex) until the 13th postnatal day, that is, the day of opening the eyes, but later on with negative allometry.

Now, a comparison of adult rodents of different body size shows that some of these growth gradients have remained similar in the different spe-

cies, whereas others have been markedly altered in phylogeny (Schulz, 1951). But apparently the relatively largest and most progressive brain region, the holocortex 7-stratificatus more or less maintains its direction of allometry, being positive until maturity, in ontogeny as well as in phylogeny. In the series white mouse-white rat-rabbit this region increases from 37.2% to 39.8% and 42.0% of the whole cortex (differences statistically valid). The semicortex on the contrary, growing isometrically or with negative allometry, decreases in the above series: mouse 18.7%—rat 13.9%—rabbit 9.0%.

Quite recently similar inquiries on races of domestic fowl of different body size were performed. Schlabritzky (1953) showed that in five races of different size the correlation of brain weight to body weight remains constant in ontogeny, that is, young individuals of dwarfs have the same rela-

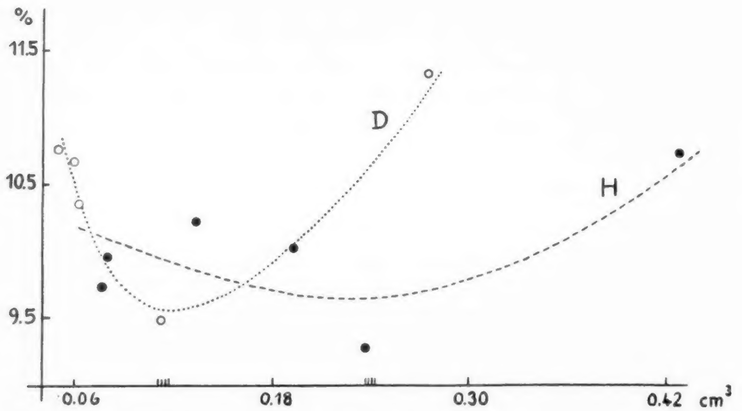

FIGURE 1. Correlation between the relative volume of the neostriatum (ordinate) and the absolute volume of the striatum (abscissa) in races of domestic fowl. H = New Hampshire, D = dwarfs. (After Krumschmidt).

tive brain weight as young chickens of giants being of equal body size. In spite of this fact the histologically different brain regions do not grow isometrically with the whole brain, but show different growth gradients. Especially the Neostriatum, which is so typical for the bird brain, grows with positive allometry (figure 1), whereas the cortical regions grow with negative allometry (figure 2). (Krumschmidt, in press). Hence also in closely related birds, for example, races of domestic fowl of different body size, marked differences exist in the proportions of the forebrain and therefore differences in behavior can be expected. The same holds good for lizards (Rose, unpublished).

Also the postnatal growth of the forebrain of newts is not isometrical in all its parts, but the Area dorsalis and the A. medialis grow more or less with positive allometry. The Striatum on the contrary grows with negative

allometry, while the Epistriatum grows isometrically (Homeyer, 1951). Corresponding to this fact, related species of newts and salamanders show different proportions of their brain regions: in large species the Area dorsalis is relatively larger, and in the mid brain the cell layers of the Tectum opticum are more numerous (Nolte, 1953).

As an example taken from fishes Wellensiek (1953) analyzed the brains of Cyprinodontidae of different body size. Here the smallest species have a relatively large mid brain and a relatively very large Tectum opticum, whereas the forebrain is relatively small.

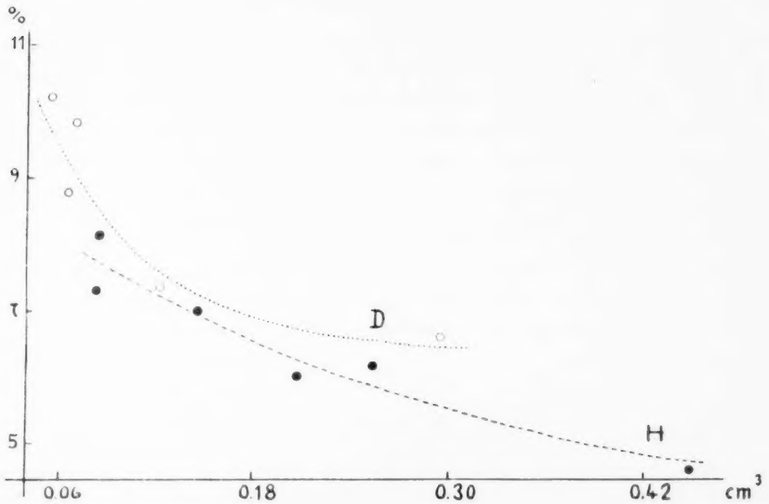

FIGURE 2. Correlation between the relative volume of cortical areas (ordinate) and absolute volume of the hemisphere (abscissa) in races of domestic fowl. H = New Hampshire, D = dwarfs. (After Krumschmidt).

Now, all these histological differences in larger and smaller species of the same relationship are further increased by cytological differences. Generally, in larger species the neurons of the brain are absolutely larger and the ganglionic layers are less wide than in smaller species. The neurons also show more dendritic ramifications, which are particularly conspicuous in pyramidal cells, but also in nerve cells of the body (Levi, 1925; Bok, 1936; Bok and van Erp Taalman Kip, 1939; Rensch, 1947; 1949; 1953; 1954; Nolte, 1953; Spina Franca Netto, 1951; Tower, 1954).

Furthermore it is important for the evolution of behavior that the increase in body size by selection (Cope's rule) often improves the function of the sense organs. Here it may be sufficient to refer to the histological structure of eyes. Normally large species have more sense cells than smaller species (among insects more ommatidia), and the percentage of rods and

TABLE 1

TOTAL NUMBERS OF NEURONS AND SENSE-CELLS IN THE RETINA OF FOUR SPECIES OF EUROPEAN NEWTS AND SALAMANDERS OF DIFFERENT BODY SIZE. (AFTER A. MÖLLER).

Species	Diameter of eye	Total number of ganglion cells	Total number of rods and cones
Triturus vulgaris	2.2mm	193 600	171 300
Triturus cristatus	2.7mm	207 500	224 300
Salamandra atra	3.3mm	316 500	386 300
Salamandra maculosa	5.5mm	308 300	533 000

cones and the numerical relation of sense cells, bipolars and cells of the ganglionic layer is shifted parallel with body size (table 1). This holds good for fishes, amphibians, birds and mammals (Bucciante and de Lorenzi, 1930; Burckhardt, 1931; Rensch, 1947; 1948; 1954; Möller, 1950; Müller, 1952, Wellensiek, 1953). Larger species thus show a better dissolving capability of the retinal image and perceive smaller parts of a complex stimulus pattern. Moreover the flatter lens of larger mammals allows a better accomodation (Rensch, 1947, 1948, 1954).

Finally, we have to take into consideration that a selection which alters body size, also alters the relative size of many hormone glands influencing the behavior, (Jackson, 1913; Riddle, 1927, Oboussier, 1948; Padour, 1950; Schlabritzky, 1953).

EFFECTS ON VERTEBRATE BEHAVIOR

Now, all the above differences between larger and smaller related animals, differences of the relative size of certain brain parts, of single cytoarchitectonic regions, of the size of neurons and of their ramification, of sense organs and of hormone glands can affect the behavior. To prove this, we compared large and small related species or races of fishes, birds and mammals and got more or less similar results in all groups.

Larger species are generally slower, more "thoughtful," more steady in behavior, because of their less intense metabolism (Rensch, 1947, 1954). This holds good for Cyprinodontidae, for races of domestic fowl, for large and small parrots, for rodents, etc.

At least in some cases the instincts of larger species are more complicated than those of related smaller species. Among grouse the courtship is more complicated in Tetrao and Lyrurus than in the smaller Tetrastes; in the large bustard *Otis tarda* more complicated than in the small *O. tetrax*; in the large grebe *Podiceps cristatus* more complicated than in the small *P. ruficollis*. Young rats show playing instincts, young mice do not play (Eibl-Eibesfeld). But with respect to the enormous complication of brain structure in all vertebrates, also in small ones, it is doubtful, whether a corresponding rule of more general applicability exists.

But the learning capacity is generally larger in larger species. In Cyprinodontidae of different body size (Xiphophorus and Lebistes) the larger species did not learn more visual tasks, but the experiments have to be repeated with more individuals (Rensch, 1954 a,b,c). Altevogt's investigations in races of domestic fowl of different body size and thus different absolute brain size (1951) were rather striking. Large races succeeded in mastering six visual tasks (discrimination pairs like red against green, black circle against black triangle, square against cross, etc.). A dwarf race only mastered four such tasks (one individual five tasks for a short time). Apparently there are similar differences between related species of different body size of other families of birds, as the (averbal) counting experiments by Koehler and his school proved. The best budgerigar (Melopsittacus) of Marold (1939), for instance, learned to eat 2, 3 or 4 grains according to three differently colored patterns arranged in front of the food boxes. But a large Amazon parrot of Brauns (1952) even learned to find the right pattern out of five food boxes corresponding to either three, four, five, six or seven spots on a cardboard shown as a "signal" in front of the food boxes. And in these experiments the spots on the "signal" cardboard needed not have the same size and arrangement as those on the cardboards covering the food boxes. A similar task was mastered by a raven of Koehler (1943), whereas the smaller jackdaws of Schiemann (1939) only learned to eat two or four mealworms, when a similar "signal" cardboard indicated two or four spots.

A corresponding comparison of rats and mice did not reveal such differences in the quantity of learned tasks during the first series of experiments (von Boxberger, 1953). Both species learned to discriminate six pairs of patterns arranged successively in a running way. They had to pass a flap door with the positive pattern six times and had to avoid a locked door with the negative pattern. The succession of patterns and the positive side were always changed. When a seventh task was added, neither species succeeded. But as the rats ran more "blindly" and the mice were more cautious and as they were more attracted by the food, I had Miss W. Reetz repeat these learning experiments with similar patterns, but applying Lashley's jumping method, because here the psychological conditions were more alike for both species. The size of the patterns and the jumping distance were chosen proportionately to the body size of rats and mice. It was interesting that these experiments had other results (still unpublished). Now the rats learned nearly all tasks more quickly than the mice, and they also learned more tasks. In the serial rotation test with five tasks both species gave nearly equal results, but the test with seven tasks was mastered by all five rats, but only by one of the mice. Three rats even learnt eight tasks (data statistically valid), whereas the last mentioned mouse had forgotten one of the tasks (table 2).

As the learning capacity seemed to be correlated with the absolute brain size, it was of interest to examine the terrestrial mammal having the larg-

TABLE 2

MULTIPLE TESTS OF RATS AND MICE. IRREGULAR SERIAL ROTATION OF 6–8 PAIRS OF PATTERNS. EACH PAIR TESTED 50 TIMES IN EACH SERIES. PERCENTAGE OF RIGHT CHOICES. (AFTER W. REETZ).

Patterns	6 tasks		7 tasks		8 tasks	
	5 rats	5 mice	5 rats	1 mouse (of 5)	3 rats (of 5)	1 mouse (of 5)
square-cross	85	86	91	84	90	76
white-black point	94	96	98	84	96	98
wave-stripe	82	80	87	72	91	(38)
dark-white ring	75	79	85	84	82	94
triangle-2 stripes	85	75	82	90	92	80
coarse-fine stripes	99	96	99	100	99	100
cheque-oblique spot	....	....	82	84	92	78
angle-points	....	....	....	....	97	94

est brain (about 6000 g), the elephant. And indeed, the capacity was surprisingly great in this animal (Rensch and Altevogt, 1953, 1955). We trained a young female Indian elephant (5–6 years old) to discriminate between a pair of patterns, positive choice rewarded. The first task was a black cross against a black circle. As soon as the task was learned we trained the animal to discriminate a new pair of patterns. After several pairs of patterns had been learned, we tested the animal, whether it mastered all tasks in serial rotation, when patterns and positive side were

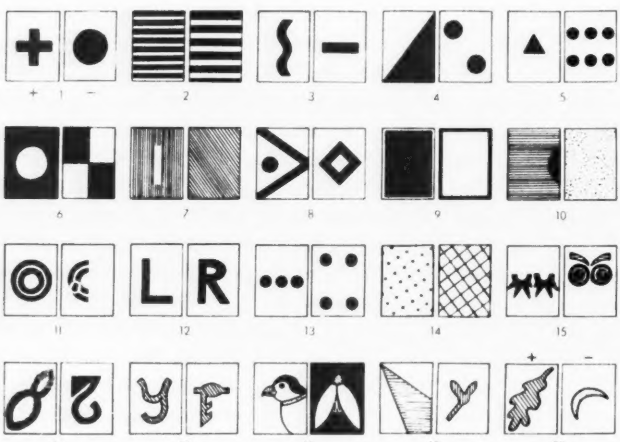

FIGURE 3. 20 pairs of patterns, which a young Indian elephant mastered in serial rotation. Each positive pattern to the left. (After Rensch and Altevogt).

TABLE 3

MULTIPLE TEST OF YOUNG ZOO-ELEPHANT. 20 LEARNED PAIRS OF PATTERNS IN IRREGULAR SERIAL ROTATION. 30 TRIALS OF EACH PAIR OF PATTERN. (AFTER B. RENSCH AND R. ALTEVOGT).

Pairs of patterns			Percentage of right choices
1. cross	against	circle	93% ±4.7
2. fine	"	coarse stripes	100%
3. snake line	"	stripe	87% ±6.1
4. oblique triangle	"	2 points	100%
5. triangle	"	6 points	97% ±3.1
6. white point	"	cheque	100%
7. red	"	green	83% ±6.9
8. angle	"	rhombus	80% ±7.3
9. black	"	white	97% ±3.1
10. blue	"	yellow	100%
11. double ring	"	2 half rings	100%
12. L	"	R	80% ±7.3
13. 3 points	"	4 points	100%
14. many points	"	grid	93% ±4.7
15. closed	"	opened eyes	97% ±3.1
16. 8	"	z	100%
17. y (green)	"	note (green)	93% ±4.7
18. parrot	"	snowdrop	100%
19. blue wedge	"	red hare	87% ±6.1
20. oak leaf	"	crescent	97% ±3.1

changed irregularly. Finally, the elephant mastered 20 pairs of patterns (figure 3). In one large test she stood 600 trials resulting in 80–100% correct choices for each pair of patterns (data statistically valid, table 3). By simultaneous presentation of one positive and three negative patterns we could prove that the elephant knew all the 40 patterns singly as positive or negative ones (figure 4). Another co-worker has just begun comparative experiments with other ungulates.

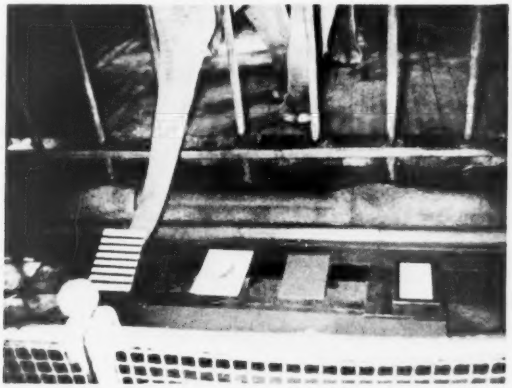

FIGURE 4. Simultaneous presentation of one positive (stripes) and 3 negative patterns (crescent, green, white with black margin) to an Indian elephant. (After Rensch and Altevogt).

Corresponding with this astonishing learning capacity, also the acoustic learning ability is very highly developed in elephants, as we could show in India (Rensch and Altevogt, 1955 b). Older animals between 30 and 60 years of age react to 21–23 different verbal commands (given in Urdu language) by purely auditory perception. Their corresponding actions often were very plastic and adapted to the special situation. At present the zoo elephant mentioned above has learned to discriminate between 12 different tones produced by a tone generator three of them differing only by one step), six of them being rewarded. (Reinert, unpublished).

But large animals also retain for a longer period than related smaller species. This could already be shown in Cyprinodontidae. Two series of *Xiphophorus helleri* (two and five specimens) retained a learned task (.... against :) for 54 and 30 days (on the average); two series of the smaller *Lebistes reticulatus* (four in each series) not even for three days (Rensch, 1954 b) (table 4). After 20 days without training a giant race of domestic fowl mastered six pairs of pattern, learned before, whereas a dwarf race only mastered three–five tasks. Five younger white rats retained a visual task three weeks longer (on the average) than five white mice of a physiologically similar age. The best rat trained by Reetz retained eight pairs of patterns for 33 days, four pairs of patterns for 154 days, one pair of patterns for 459 days, whereas the best of the correspondingly trained mice only mastered four pairs of patterns after 103 days and one pair of patterns after 195 days (controlled at intervals of four weeks; always 10 trials without reward). After a period of one year without training the zoo-elephant recognized 12 tasks of 13 tasks learnt before, but also in the 13th task she made 67% of right choices, this datum being nearly statistically valid (520 choices within three hours, each pair of patterns presented 40 times in an irregular sequence, table 5).

TABLE 4

RETAINING TEST IN TWO SERIES (A,C) OF CYPRINODONTIDAE OF DIFFERENT BODY SIZE. TRAINED TASK: FOUR POINTS HORIZONTALLY (POSITIVE) AGAINST TWO POINTS VERTICALLY (NEGATIVE). AVERAGES OF PERCENTAGE OF RIGHT CHOICES. EACH TIME 10 TRIALS WITHOUT REWARD.

Days after last training experiment	3	17	27	44	54	64
A. 2 Xiphophorus	75	90	85	70	80	45
4 Lebistes	67	40	35	56	27	20
Days after last training experiment	0	19	30	41		
C. 5 Xiphophorus	94	84	65	53		
4 Lebistes	92	58	60	27		

TABLE 5

RESULTS OF A RETAINING TEST OF A YOUNG ELEPHANT FOR 13 LEARNED PAIRS OF PATTERNS AFTER ONE YEAR WITHOUT TRAINING. PATTERN HERE IN SUCCESSION OF LEARNING. EACH PAIR OF PATTERNS TESTED 40 TIMES IN IRREGULAR SERIAL ROTATION. (AFTER B. RENSCH AND R. ALTEVOGT).

Pair of pattern			Percentage of right choices
1. cross	against	circle	90% ±4.8
2. fine	"	coarse stripes	90% ±4.8
3. snake line	"	stripe	73% ±7.0
4. oblique triangle	"	2 points	97% ±2.7
5. triangle	"	6 points	100%
6. white point	"	cheque	95% ±3.4
7. red	"	green	95% ±3.4
8. angle	"	rhombus	67% ±7.5
9. black	"	white	80% ±6.3
10. blue	"	yellow	97% ±2.7
11. double ring	"	2 half rings	77% ±6.7
12. L	"	R	73% ±7.0
13. 3 points	"	4 points	83% ±5.9

In transposition experiments, that is, by alteration of the learned patterns, the rats of Miss Reetz were markedly better in five tasks than the mice, the latter were only better in one task. The elephant was also able to recognize far-going alterations of the learned patterns. In the Cyprinodontidae corresponding experiments did not show clear differences between the larger and the smaller species.

SUMMARY & CONCLUSIONS

Summarizing all the results we may state that in vertebrates larger species, that is species with absolutely larger brains, are able to learn more (and apparently also more complicated) visual tasks and to retain them for a longer period than comparable related species of smaller size. The capability of abstraction (transposition) has not yet sufficiently been examined. The differences obtained correspond in some respect with the statements of Lashley (1931) and Layman (1936), that the capacity for learning is proportionate to the mass of the forebrain, when this is reduced by operation.

With regard to the intact animals of our experiments I would presume that an increase of the learning capacity in larger species is due to the absolutely larger neurons and the correlated increase in number of dendrites effecting a more complex switch mechanism. The capacity of larger animals to retain for a longer period is perhaps also due to the larger cell size allowing a stronger histological connection as a basis of associations. Of course many experiments will be needed to confirm the mentioned results and hypotheses.

APPLICATION TO EVOLUTION

As regards *evolution* these statements are especially important, because they show that all purely quantitative increase of the numbers and of the

size of neurons can be a selective advantage, for it is doubtlessly advantageous to learn more and more complicated actions and to retain for a longer time. Thus the rule of progression of the brain becomes intelligible and one of the factors (besides others), explaining Cope's rule of successive phyletic increase of body size becomes clear.

Apparently the development of behavior follows the morphological alterations of the brain. In our case this would mean: at first probably new brain regions were developed phylogenetically by positive allometry of progressive parts, and later on these parts became successively filled with functions of behavior. Such a working hypothesis can be supported by several facts, which I will indicate only shortly.

1) In the lowest vertebrates the cerebellum is developed as an additional centre. In sharks it is already rather large, but extirpation is not very effective. In birds the Lobus medius is more developed, but does not seem to have any specific functions yet. 2) In amphibians the forebrain is already relatively large, but is still fairly unimportant, as proved by extirpation experiments. Moreover, the studies by Nolte (1953) suggest that in amphibians especially the positive allometry of the Area dorsalis, a region where no important functions seem to be localized, would be the basis of an improved development of a future cortex. 3) After centres for all senses had developed in the vertebrate brain, additional regions arose and now could be used as centres of association. The same holds good for the Corpora pedunculata of the polychaetes and arthropods as well as for the frontal and temporal lobes of mammals. This is especially so with Broca's region of the human brain, which could be filled additionally with motor functions of speech, thus contributing to the rapid development of human culture. And apparently, the brains of higher vertebrates are capable of many more functions than are usually required in their normal life. This becomes evident from the astonishing performances of trained animals, for example, the averbal counting ability of birds. Therefore all higher vertebrates perform many "unneccessary" actions during their life (sometimes similar to playing). All this seems to indicate that the enlargement of the brain normally happens by the formation of new regions, which become filled with functions only successively.

EVOLUTION OF BEHAVIOR

When we now try to view these problems from an aspect of the evolution of behavior as a whole, similar conclusions are possible. We may state that the selective alterations often happen in the sense of an "addition to the final stages." In different lines of descent, especially in vertebrates, the increasing complication often is brought about by additional complexes of neurons becoming centres of a higher order. At first the mid-brain developed as a main centre of association. Afterwards this function was shifted to the subcortical regions of the forebrain, then to the cortex. Here

at first the sensory and motor regions served this function and finally the larger centres of association became active. Also in annelids and arthropods a corresponding improved development resulted in the formation of larger association centres in the Corpora pedunculata. Corresponding with this course of development at first reflexes and deflexes (plastic reflexes) developed, then rigid or more plastic instincts arose, after which actions based on learning processes (engrams), on abstractions or on insight (comprehending causal connections) could be developed. The driving force of this improvement was the advantage of an increasing adaptation to the complicated stimulus situations of the habitats, that is, to the extra-subjective realities (cf. Rensch, 1954a).

It is remarkable that very different histological systems, the midbrain of fishes, the subcortical regions of birds, and the cortex of mammals, enabled the animals to attain the same capacities of learning, retaining and abstracting. [Learning in the sense of conditioned reflexes, can already be performed by the spinal cord of amphibians: Franzisket, 1951, Rensch and Franzisket, 1954, Rensch, 1952].

If we now ask, *why* this development was more or less an addition to the final stages and not an "archallaxis" (Sewertzoff, 1931), that is, an alteration already beginning with the first ontogenetic stages, the answer will be similar to that concerning the development of other organs. After a harmoniously working structural type had developed in phylogeny, it was easier that variants survived, in which a new development was added to the final stages, because all earlier alterations would more disturb or destroy the established harmony.

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GENERATION TIME AND THE BIOLOGICAL NATURE OF VIRUSES

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INTRODUCTION

Whether or not viruses are to be regarded as organisms or chemicals is a matter of disagreement or of point of view (Stanley, 1938; Burnet, 1945). If it could be shown that the rate of reproduction of conventional organisms shows a quantitative relation to their size, and if it could be shown that our present knowledge of virus size and rate of reproduction fits into this quantitative relation for conventional organisms, this would constitute evidence that viruses are organisms. Such is attempted here.

No previous study of this type has been found. Evans and Smith (1952) give times for doubling of populations of two rodents and three insects with data which support the absolute data and the trend presented in table 1 and figure 1 of the present study, but these authors do not point out any relation between body size and generation time. Elton (1927) states the well known fact that small animals increase faster than large ones, but does not present quantitative evidence.

METHODS

Size is given as the fresh weight of the adult organism. With small organisms this is calculated from microscopic measurements and known or assumed densities. With viruses it is assumed that the bodies seen in the electron microscope are the adult forms. Generation time is given as the time for a population to double under what are believed to be near optimum conditions for reproduction. Since most organisms and some viruses reproduce in cycles with multiple progeny, the generation times do not correspond to the time for a normal generation or cycle. Generation time is calculated as:

$$\frac{\text{time X logarithm of 2}}{\text{logarithm of increase in population}}$$

from known or estimated rates of increase. Time is the interval in minutes during which increase in population was studied. Increase in population is the proportional increase in numbers. For example, Chapman (1928) found that a colony of flour beetles (*Tribolium confusum*) increased from 2 to 4500 individuals in 154 days. Time would then be $154 \times 24 \times 60$ minutes,

[1]The assistance of O. P. Pearson in securing the data for mammals is gratefully acknowledged.

TABLE 1

SIZE AND RATE OF REPRODUCTION OF VIRUSES AND CONVENTIONAL ORGANISMS.

Virus or organism	Body Weight	Authority for body weight	Generation time	Authority for generation time
	grams		*minutes*	
Foot and mouth disease virus	5×10^{-19}	Rhodes et al., 1953	5×10^{1}	Henderson, 1953
Tobacco necrosis virus	5×10^{-18}	Stanley, 1947	1×10^{2}	Yarwood, 1952
Southern bean mosaic virus	1×10^{-17}	Stanley, 1947	2×10^{2}	Yarwood, 1955
Tobacco mosaic virus	7×10^{-17}	Stanley, 1947	6×10^{1}	Yarwood, 1952
T_2 coli phage	2×10^{-16}	Rhodes et al. 1953	5×10^{0}	Adams 1950
T_5 coli phage	8×10^{-16}	Weigle et al. 1951	1×10^{1}	Weigle et al. 1951
Influenza virus	1×10^{-15}	Stanley, 1947	6×10^{1}	Horsfall, 1953
Escherichia coli	3×10^{-13}	Breed et al. 1948	2×10^{1}	Mason, 1935
Xanthomonas phaseoli	1×10^{-12}	Breed et al. 1948	3×10^{2}	Allington et al. 1949
Chlorella pyrenoidosa	6×10^{-11}	Burlew, 1953	2×10^{2}	Burlew, 1953
Hansenula anomala	1×10^{-10}	Lodder et al. 1952	1×10^{2}	Grieg et al. 1941
Saccharomyces cerevisiae	2×10^{-10}	Lodder et al. 1952	1×10^{2}	Pennington et al. 1951
Colpidium colpoda	5×10^{-8}	Pratt, 1916	6×10^{2}	Cutler et al. 1923
Enchelys farcimen	6×10^{-8}	Robertson, 1921	2×10^{2}	Robertson 1921
Paramecium caudatum	5×10^{-7}	Kalmus, 1931	7×10^{2}	Gause, 1934
Monilinia fructicola	8×10^{-7}	Yarwood, 1955	1×10^{3}	Yarwood, 1955
Erysiphe polygoni	1×10^{-6}	Yarwood, 1955	5×10^{2}	Yarwood, 1955
Hydratina senta	1×10^{-5}	Hudson et al., 1889	5×10^{2}	Edmondson, 1946
Brevicoryne brassicae	1×10^{-3}	Herrick, 1926	3×10^{3}	Herrick, 1926
Tribolium confusum	1×10^{-3}	Yarwood, 1955	2×10^{4}	Chapman, 1929
Musca domestica	2×10^{-2}	Yarwood, 1955	3×10^{3}	Howard, 1924
Physa gyrina	1×10^{0}	DeWitt, 1954a	2×10^{4}	DeWitt, 1954b
Passer domesticus	2×10^{1}	Pearson, 1955	1×10^{5}	Barrows, 1889
Ostrea virginica	3×10^{1}	Pratt, 1916	2×10^{4}	Galstoff, 1930
Rattus norvegicus	2×10^{2}	Pearson, 1955	8×10^{4}	Fischer, 1972
Gallus domesticus	2×10^{3}	Robinson, 1912	8×10^{4}	Robinson, 1912
Oryctolagus cuniculus	2×10^{3}	Asdell, 1946	1×10^{5}	Fenner, 1954
Phasianus colchieus	2×10^{3}	Yarwood, 1955	2×10^{5}	Yarwood, 1955
Solanum tuberosum	3×10^{3}	Yarwood, 1955	9×10^{4}	Yarwood, 1955
Helianthus annuus	6×10^{3}	Yarwood, 1955	4×10^{4}	Yarwood, 1955
Homo sapiens	5×10^{4}	Yarwood, 1955	5×10^{6}	Malthus, 1803
Sus scrofa domestica	1×10^{5}	Asdell, 1946	2×10^{5}	Asdell, 1946
Bos taurus	4×10^{5}	Asdell, 1946	1×10^{6}	Asdell, 1946
Sibbaldus musculans	8×10^{7}	Jordan, 1929	1×10^{6}	Krogh, 1934
Pseudotsuga taxifolia	2×10^{8}	Frothingham, 1909	2×10^{6}	Baker, 1950
Sequoia gigantea	2×10^{9}	Fry et al., 1938	5×10^{6}	Fry et al., 1938

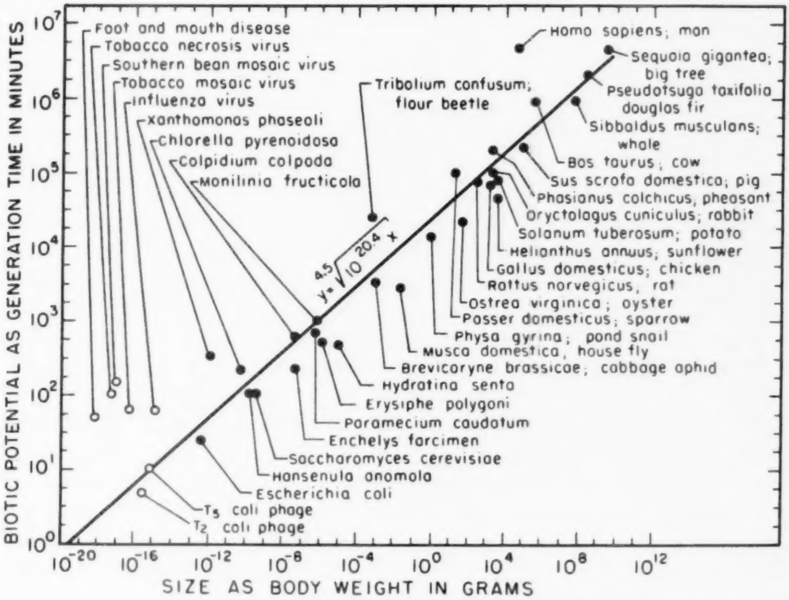

FIGURE 1. Relation of body weight to rate of reproduction.

the increase in population would be $\frac{4500}{2}$ or 2250 fold (logarithm of 2250 = 3.353) and the generation time would be $\frac{154 \times 24 \times 60 \times 0.301}{3.353} = 1.99 \times 10^4$. Because of the uncertainty and variability of values, size and generation times are given to only the nearest digit (e.g. 2320 would be given as 2×10^3).

Representative organisms from various taxonomic groups were chosen on the basis of available data, even though these data were in many cases somewhat inadequate. In several cases it was easier for me to weigh or measure a representative or group of individuals than to look for published information on body size. For the published data secondary sources were sometimes used. Reproduction rates for the 17-year locust (*Magicicada septendicim*) and the tuberculosis bacterium (*Mycobacterium tuberculosis*) were intentionally omitted because it is believed that these organisms reproduce at a much slower rate than is typical of the taxonomic groups in which they occur.

RESULTS

Results for 28 species of conventional organisms and for seven viruses are given in table 1 and figure 1. There is a fairly progressive increase in generation time with increase in body weight through many taxonomic groups

of plants and animals. That this is a straight line relation cannot be established from the limited data, but it seems a useful hypothesis. If so, the average generation time for the 28 species of conventional organisms including bacteria, algae, fungi protozoa, insects, snails, birds, mammals, herbs and trees is about $\sqrt[4.5]{10^{20.4}X}$ when X is body weight in grams. The seven viruses as a group fit fairly well into this relation of generation time to body weight for conventional organisms.

The two bacteria and seven viruses listed illustrate what may be significantly greater generation times for tissue-invading than for free-living forms. Data for *E. coli* (16 minutes generation time) is for free living forms in broth, while data for *X. phaseoli* (260 minutes generation time) is for infections in bean leaves. Several other free-living forms could be substituted for *E. coli* and several other tissue-invading forms could be substituted for *X. phaseoli*, or the generation time of *X. phaseoli* could be compared as a free living form (Mason, 1935) and as a tissue invading form (Allington and Chamberlain, 1949), with the same trend in the data. With the viruses, while all are intracellular, the phages are similar to free living forms in that they are free in the medium after the burst of each host cell, and their generation times appear significantly lower than the generation times of the tissue-invading forms. If the values presented for tissue-invading forms of bacteria and viruses could be corrected by a factor by which the tissue-invading forms and free-living forms differ, the values for tissue-invading bacteria and viruses would be closer to the value for the other conventional organisms. It is also likely that if generation times for tissue-invading viruses could be determined within single cells, the times would be much less.

It may also be noteworthy that the rate of increase has been more intensively studied with the bacteriophages than with tissue-invading viruses. As the tissue-invading forms are studied more intensively, it is likely that in the future as in the past (Yarwood, 1952) the generation times for these viruses will be found to be considerably less than the early or present values. As these values for tissue-invading viruses are reduced with further research, the body weight: generation time relation for viruses will probably fit more closely the values for conventional organisms.

SUMMARY

The generation time (time for doubling of the population) under optimum conditions for 28 conventional organisms ranging from bacteria to redwood trees increased at a fairly regular rate with increase in body weight. The average generation time was about $\sqrt[4.5]{10^{20.4}X}$ or $X^{0.227} \times 10^{4.4}$ minutes when X was the body weight in grams. The generation times of two bacteriophages were very close to this value, but the generation times for five tissue-invading viruses were much greater. On this basis and on the basis of plausible corrections for tissue-invading viruses, it is believed that the relation of body weight to rate of reproduction is basically the same for viruses as for conventional organisms.

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STUDIES ON MATERNAL RETRIEVING IN RATS: II. EFFECTS OF PRACTICE AND PREVIOUS PARTURITIONS[1]

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Many types of behavior are executed imperfectly or incompletely at the time of their first occurrence, and become perfected and efficient only as a result of practice. Some other responses appear in well-developed and effective form the first time they occur. Thus the female rat that has never built nests or born young will typically construct a nest toward the termination of her first pregnancy, and will deliver, clean, and nurse her first litter successfully. This conclusion is substantiated by the work of several investigators (Weisner and Sheard, 1933; Beach, 1937; Stone, 1938), and the biological adequacy of the primiparous mother seems well established. At the same time, there remains the possibility that maternal efficiency might improve as a result of the experience gained in successive parturitions, and care of the young might become more effective in the course of a single lactation period. The present experiment was conducted to discover whether either or both of these possibilities are reflected in fact.

SUBJECTS AND METHODS

Subjects were 19 multiparous and 18 primiparous rats of a pigmented strain. Each animal was placed in a special observation cage approximately five days prepartum and remained there until maternal tests were completed. The wooden cages were 3' × 3' × 1' and were divided by a central partition pierced by a small doorway. Connected with the outer wall of each half of the cage was a covered release box (6" × 4" × 4") separated from the main cage by a vertically sliding door. Strips of paper towelling suspended from the cage walls served as nesting material. The observation cages were situated in a quiet, darkened room, and each one was illuminated by a 40w bulb.

Each cage was inspected several times a day, and within a few hours after parturition the size of the litter was recorded. In addition notes were made of the number of young which were well or poorly cleaned. On the day of parturition the nest was photographed and rated on a five-point scale. At regular intervals postpartum the female's retrieving behavior was tested. The mother was gently removed from the cage and confined in the release box farthest from her nest. Young were picked up with forceps and placed

[1]This study was supported in part by a grant from the Committee for Research in Problems of Sex, National Research Council. The experimental observations were carried out in the Department of Animal Behavior at the American Museum of Natural History.

at predetermined locations on the cage floor. The door to the release box was raised and a timer was started when the female entered the observation cage.

In all retrieving tests records were made of the number of young returned to the nest at six standard intervals. These were .5, 1, 5, 10, 30, 60 minutes from the time the female left the release box and entered the main cage. In some of the tests notes were made of the time at which each individual pup was retrieved. A special method of recording the mother's movements about the cage was utilized upon several occasions. The cage floor was marked off into 36 equal, numbered squares, and as the female walked about, the number of each square she entered was tabulated. All retrieving tests lasted until the last pup had been retrieved or until 60 minutes had elapsed.

Ten of the primiparous females (Group I) were given a minimum of five daily retrieving tests beginning on the day of parturition. Six of these animals were also tested on the sixth day, and four on the seventh day postpartum. The remaining eight primiparae (Group II) were given only one retrieving test. For two females this occurred on the day of parturition. Three additional mothers were removed from the cage and handled briefly on the first two days, just as if retrieving tests were being conducted, and then tested for the first time three days postpartum. The final three cases were handled daily for six days postpartum, and then given the retrieving test on the seventh day after giving birth.

Ten of the multiparous rats (Group III) had previously reared litters in small breeding cages but had never been tested for nest-building or retrieving. This group was given a minimum of five daily retrieving tests beginning on the day of parturition as were Group I. The other nine multiparae (Group IV) had previously littered in the special observation cages, and had been observed in four to eight formal retrieving tests at that time. On the day of the second parturition, they were given retrieving tests and the results compared with their previous records.

RESULTS AND DISCUSSION

Parturition and retrieving behavior of multiparous and primiparous females. Comparisons of the parturient behavior of females in Groups I and

TABLE 1

VARIOUS MEASURES OF MATERNAL BEHAVIOR FOR TEN MULTIPAROUS AND TEN PRIMIPAROUS FEMALES

Group mean	Primiparous Group I	Multiparous Group III
Number of pups born	8.3	8.8
Number of pups poorly cleaned	0.5	0.7
Number of pups out of nest	0.0	0.3
Median grade of nest		
Day before parturition	3.5	1.0
Day after parturition	3.5	1.5

TABLE 2

AVERAGE CUMULATIVE NUMBER OF PUPS RETRIEVED AT VARIOUS INTERVALS FOR 10 PRIMIPAROUS (P) AND 10 MULTIPAROUS (M) FEMALES ON FIVE SUCCESSIVE DAYS AFTER PARTURITION

Time intervals in minutes of test	Day 1		Day 2		Day 3		Day 4		Day 5	
	P	M	P	M	P	M	P	M	P	M
0.5	0.8	0.4	1.1	1.3	2.7	1.9	2.9	2.8	2.8	2.8
1	1.8	1.3	2.0	2.7	4.7	3.3	4.9	4.6	4.8	4.2
5	5.3	3.9	5.0	5.2	5.9	5.2	5.9	5.8	5.9	5.5
10	5.4	5.0	5.7	6.0	5.9	5.3	5.9	6.0	5.9	5.6
30	5.8	5.5	6.0	6.0	6.0	5.5	5.9	6.0	5.9	6.0
60	6.0	5.5	6.0	6.0	6.0	5.9	5.9	6.0	5.9	6.0

III indicate that the experience of bearing and rearing one litter has no effect upon nest-building or caring for the young at the termination of a second pregnancy. The relevant comparisons appear in table 1. None of the differences are statistically reliable.

The primiparae of Group I had no experience in retrieving young. The multiparae of Group III had a somewhat comparable history in that their previous litters had been reared in small cages where necessity or opportunity for retrieving was very limited. The retrieving behavior of these two

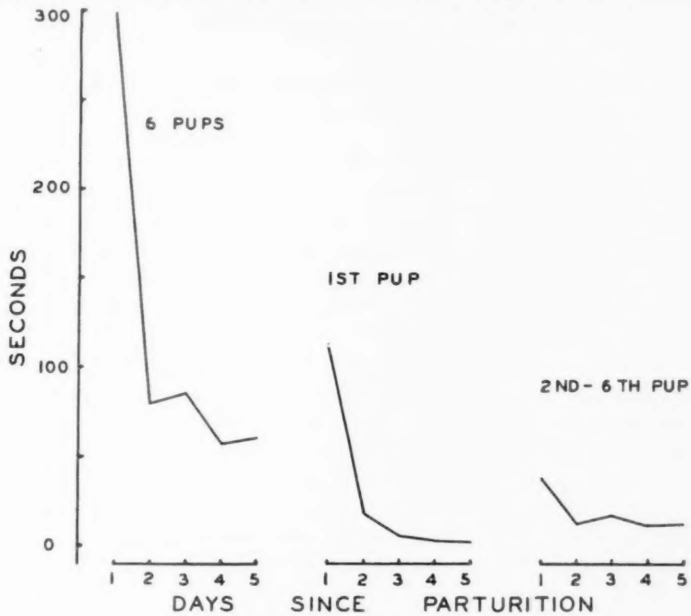

FIGURE 1. Median total time to retrieve all six pups, median time to retrieve the first pup only, and the average of the median times to retrieve the 2nd, 3rd, 4th, 5th, and 6th pups, on five successive days following parturition.

types of females is compared in table 2, and it is evident that no appreciable differences existed.

Day-to-day changes in retrieving. Table 2 does show an improvement in retrieving performance on successive daily tests, and the rate of change is comparable for multiparous and primiparous females. Combining the averages for the two groups, on the day of parturition an average of 1.6 pups were retrieved during the first minute of the test. By the fifth day postpartum performance had improved to the point that an average of 4.5 young were retrieved to the nest in the first 60 seconds. Comparing the number of pups retrieved during the initial 60 seconds of the first and fifth tests, increases in this score were found for 18 females and there was no change in the remaining two cases. This group increase in rate of retrieving is therefore statistically reliable by the sign test at the one per cent level of confidence.

Figure 1 reveals one source of the changes responsible for increases in the speed of retrieving. This figure is based on records of the seven animals for which the retrieving time of each pup was recorded. It is apparent that most of the day-to-day acceleration in total retrieving was due to a decrease in the delay preceding retrieving of the first pup. No appreciable change occurred in the time taken to complete the retrieving of the remainder of the young once retrieving had started. Furthermore, most of the increase in speed of retrieving the first pup took place on the second day postpartum.

In the case of eight animals (4 from Group I and 4 from Group II) records were kept of the female's movements about the cage during the retrieving test. The number of squares entered from the beginning to the end of the retrieving test tended to decrease on successive days. On the first day postpartum, an average of 110 squares was entered. On succeeding days this value was 82, 85, 73, and 63. The progressive decrease in the number of squares entered suggests a second sort of change responsible for increased speed of retrieving, namely that females tended to engage in less exploration either before beginning to retrieve or during intervals between the retrieving of successive pups.

Retrieving in unpracticed primiparae. Changes in the speed of retrieving could be due to factors other than practice. Firstly, females might become progressively stronger and more active for several days after giving birth. Secondly, the fact that young increase in size and motility might make them more prominent stimulus objects to be approached and retrieved. Thirdly, adaptation to handling by the experimenter could account for considerable improvement, particularly in the speed with which retrieving was begun. For these reasons, the results of tests on primiparous rats in Group II are important.

These animals were given their first retrieving test on the first, third, or seventh day postpartum, and were handled daily up to the day of testing. The results showed no significant difference in the retrieving behavior of

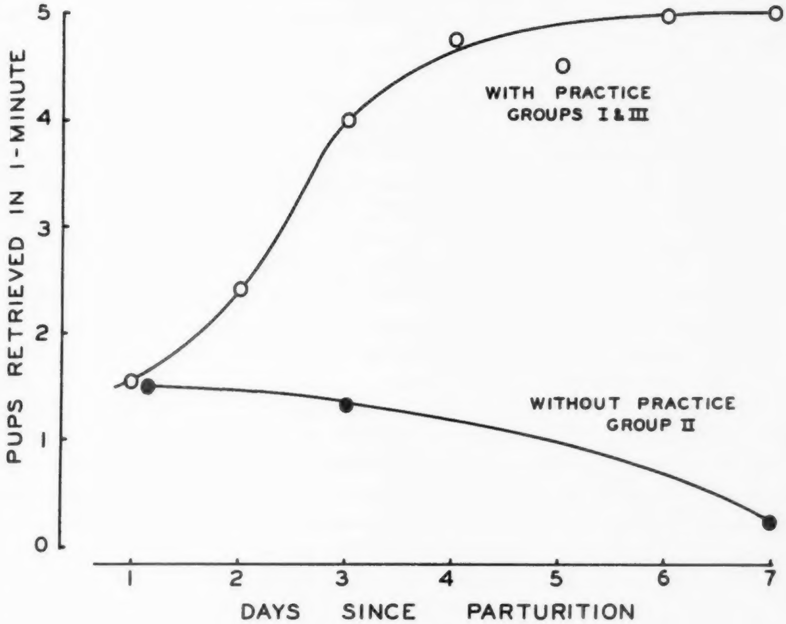

FIGURE 2. Retrieving with and without practice as a function of days since parturition.

females receiving their first tests at these three intervals after parturition. The average number of pups retrieved within the first minute is shown in figure 2 where the scores of animals in Group II are compared with the combined scores of Groups I and III. Differences between the performance of mothers with practice and without practice are statistically reliable, despite the small number of animals in the three subdivisions of Group II. On both the third and seventh days, the P value is less than .03 by the Mann-Whitney U test. Apparently, improvement shown during successive days of

TABLE 3

CUMULATIVE SCORES SHOWING AVERAGE NUMBER OF PUPS RETRIEVED AT SUCCESSIVE INTERVALS ON THE FIRST DAY POSTPARTUM

Min. from start of test	Group I First pregnancy	Group IV First pregnancy	Group IV Second pregnancy
0.5	0.8	0.4	0.7
1.0	1.8	0.9	1.3
5.0	5.3	4.4	3.4
10.0	5.4	5.4	3.6
30.0	5.8	5.4	4.1
60.0	6.0	5.7	5.1

retrieving cannot be referred solely to changes in the young, to the time elapsed since parturition, or to effects of handling on successive days.

Retrieving in successive parturitions. Females in Group IV were tested for retrieving in two successive lactation periods. Their performance did not change significantly from one pregnancy to the next. The average number of young retrieved at the end of each of the standard time intervals is shown in table 3 where the performance of Group I is included for purposes of comparison. It is evident that the performance of Group IV during the second pregnancy was not superior to that of the same females during their first lactation period or to the retrieving of the primiparous mothers in Group I. As measured by the number of pups retrieved during the first minute of the test, 6 of the nine subjects in Group IV showed poorer retrieving following the second pregnancy, three improved and the final case showed no change in the behavior.

Two major conclusions are indicated by the results of this study. First, the retrieving behavior of lactating female rats improves if they are tested once a day starting on the day of parturition. Part of the improvement consists of a shortening of the delay preceding the retrieving of the first pup. Another feature is a reduction in the amount of territory covered in the course of retrieving the entire litter. Reduction of the initial delay is most pronounced between the first and second test. Decrease in total distance travelled occurs progressively over a series of five daily tests.

The second major conclusion is that the maternal behavior of primiparous and multiparous mothers does not differ significantly. Experience in giving birth, nest-building and retrieving during one pregnancy and lactation period has no effect upon maternal performance in a second reproductive episode.

SUMMARY

The maternal behavior of 19 multiparous and 18 primiparous rats was compared. Females that had previously born and reared litters did not differ significantly from primiparous animals in prepartum nest-building or cleaning of the young at the time of parturition. Some multiparous individuals had been given special retrieving tests during their first lactation period. Following a second pregnancy the retrieving behavior of these individuals differed in no appreciable way from that of other females which had just delivered their first litter.

When multiparous and primiparous females were observed in a series of daily retrieving tests their behavior improved, and the course of improvement was the same for both groups. Various controls indicated that this improvement was not due to changing qualities of the growing young. Increased efficiency of retrieving could be traced to two kinds of change. The first consisted of a rather sudden decrease in the delay preceding the initiation of retrieving once a test had begun. This period of delay was marked in the first test but was greatly reduced on the second day and on

all days thereafter. A second change involved a reduction in the amount of locomotor activity associated with retrieving. On successive tests the females tended to proceed more and more directly to the scattered pups and to retrieve them with a minimum of interpolated exploration of the cage.

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MUTATIONS AT A SINGLE LOCUS IN THE WASP MORMONIELLA

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In the wasp Mormoniella with haploid males from unfertilized eggs, diploid females from fertilized, many recessive eye-color mutants have been found ranging from dark red approaching the dominant wild-type brown through bright reds, orange, peach and tinged to oyster white (colorless). Irradiation of unmated females induces mutations in the eggs resulting in mutant sons in frequencies as high as one per cent of survivors. Spontaneous mutation is rare in pure stocks but frequently occurs in pedigrees after crossing different stocks. The majority of eye-color mutants occur at a certain locus, *R*, but many are scattered, segregating independently or showing linkage.

Several studies have already been made by this (first) method of breeding unmated irradiated females and dose-action curves have been obtained for X-rays and for fast and slow neutrons (Ray and Whiting, 1954, Kayhart, in press). The visible eye-color mutations resulting are all viable because recessive lethals are filtered out by male haploidy.

In order to recover recessive lethals which have visible effects in compounds and to restrict observations to the *R* locus alone, a second method has been devised making use of an *R*-locus recessive gene called peach-333.5, *pe*-333.5. Other genes causing peach eye color occur both at the *R* locus and at other loci, but peach-333.5 is the only eye-color tester gene employed in the present discussion, where it will be called simply peach or *pe*.

Because peach is an *R*-locus recessive gene any mutant-type daughters will indicate an *R*-locus mutation induced in the treated wild-type egg. The irradiated wild-type females are mated immediately after treatment to untreated peach-eyed purple-bodied males. Purple is linked with *R* giving ten per cent crossovers. Most of the offspring from this cross will be wild type, the females heterozygous, $\frac{+\quad +}{pe\quad pu}$, the males azygous, $\frac{+\quad +}{}$. A scarlet-eyed female, $\frac{st\quad +}{pe\quad pu}$, would indicate that a mutation was induced

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allelic with peach. A mutation to peach would result in a peach female, $\frac{pe\ \ +}{pe\ \ pu}$, or a peach male, $\frac{pe\ \ +}{\quad}$.

In study of mutations it is important to consider other exceptional types. If a peach purple female, $\frac{pe\ \ pu}{pe\ \ pu}$, or male, $\frac{pe\ \ pu}{\quad}$, should appear it would be highly unlikely that this would be due to mutation at the two loci. A large deficiency might result in a peach purple female, $\frac{-\,Df\,-}{pe\ \ pu}$, but androgenesis would be a more probable explanation. Androgenesis, development from the sperm nucleus alone without fusion with egg pronucleus, has been reported after X-radiation of females in Mormoniella (Friedler and Ray, 1951). In the wasp Habrobracon androgenesis occurs when the egg pronucleus is inactivated by irradiation (Whiting, Anna R., 1948). An androgenetic daughter or son is not the offspring of the female that lays the egg. Shell, yolk and egg cytoplasm are but the pre-hatching food and environment, just as host pupa and puparium or caterpillar are the post-hatching food and environment of this motherless anomaly. Its "brothers" are not its brothers for they are impaternate while it is immaternate.

The bright eye colors have been selected for study of mutation rates because these are so strikingly different from wild-type brown that they cannot be missed. It may also be safely assumed that they are true mutants since all that have been tested have proved to be such. With good light and against a dark background, dark red eye colors are easily identified but these grade into reddish brown and some of them are fluctuations of wild type. They are, therefore, not included in calculating mutation rates. The present paper reports results obtained by the second method. Wild-type females of Woods Hole stock were X-rayed and then crossed to peach purple males.

PRESENTATION OF DATA

Experiment 1. The first experiment was carried out by the junior author. Offspring per female set were 44.8 for the 98 control females, 5.6 for the 166 females treated with 3000 r and 3.5 for the 1267 females treated with 3500 r. No androgenetic offspring were produced. No mutants occurred in the controls (1798 females, 2593 males). From treated females there were 22 bright eye-color mutants (4 tomato, 11 scarlet, 4 peach, 3 oyster) among the 1807 males and 36 (1 tomato, 23 scarlet, 3 peach, 9 pale peach) among the 3599 females. Of the 14 male mutants successfully mated, 7 (4 tomato, 2 scarlet, 1 peach) sired wild-type daughters suggesting loci other than *R*, and 7 (4 scarlet, 3 oyster) gave mutant-type daughters indicating *R*.

The pale peach female mutants are oyster-peach compounds, $\frac{oy\ \ +}{pe\ \ pu}$, in-

dicating mutation to oyster in the treated eggs. Four were bred producing many oyster and peach purple (parentals), few oyster purple and peach (crossovers) sons.

Of the nine scarlet mutant females that were bred, six, $\frac{st\ \ +}{pe\ \ pu}$, produced many scarlet and peach purple (parentals), few scarlet purple and peach (crossovers) sons. These six mutations were scarlet viables.

The other three scarlet mutant females tested produced no scarlet sons but only peach (peach purple parentals, peach crossovers). These were scarlet lethal mutants because the scarlet gene here has a recessive lethal effect. A scarlet lethal female, $\frac{stl\ \ +}{pe\ \ pu}$, crossed to a peach purple male produces daughters:- scarlet, $\frac{stl\ \ +}{pe\ \ pu}$, and peach purple, $\frac{pe\ \ pu}{pe\ \ pu}$, many (parentals) and scarlet purple, $\frac{stl\ \ pu}{pe\ \ pu}$, and peach, $\frac{pe\ \ +}{pe\ \ pu}$, few (crossovers). From her unfertilized eggs, as from the eggs of an unmated female, there are produced only peach purple, $\underline{pe\ \ pu}$ (parentals) and peach, $\underline{pe\ \ +}$ (crossovers) males, because those carrying scarlet lethal, $\underline{stl\ \ +}$ and $\underline{stl\ \ pu}$, are inviable.

Rate of mutation at the *R* locus alone including recessive lethals, 2.93×10^{-6} per r, as shown in the females, is not significantly lower than rate at all loci together if lethals are not included, 3.58×10^{-6} per r, as shown by the males. The identification of haplo-inviable mutations in the *R* locus when the former method of testing for mutation rate was used demonstrates the value of this method.

Experiment 2. The senior author carried out a second experiment with the same stocks. Wild-type females, 2850 in number, were X-rayed (3500 r) and crossed with peach purple males. The purpose of this experiment was not to determine mutation rate, but rather to obtain mutants for genetic analysis. Therefore number of offspring was not counted. However, a rough estimate was made. This estimate, 10,000 from 2850 mothers, proved very close to the average number, 3.5, of counted offspring per female X-rayed with 3500 r in the earlier experiment by the junior author.

Among the males there was one peach-eyed. He was probably androgenetic rather than a mutant since he had the paternal purple body color. Among the females there were seven peach purple, androgenetic. There appeared 19 bright eye-color mutants (2 tomato, 1 vermilion, 7 scarlet, 2 peach, 7 oyster) among the males (viables at any eye-color locus) and 10 (2 pale peach, 7 scarlet, 1 dahlia) among the females (viables and recessive lethals at *R* locus only).

Daughters were obtained from seven of the nineteen bright-eyed mutant males,- the single vermilion, 2 scarlet, 1 peach and 3 oyster. Tests made by crossing these males with bright eyes to peach purple females showed peach purple sons as expected from unfertilized eggs. Because none of the daugh-

ters was wild type, these seven mutations occurred at the *R* locus. Daughters of the peach mutant were exactly like their peach purple brothers in eye color and in F_2 the mutant peach could not be separated from peach-333.5. In contrast, the pale peach daughters of each of the three oyster mutants were distinctly lighter than their peach purple brothers and the expected difference was noted among the F_2 females. The vermilion and scarlet males sired vermilion and scarlet daughters respectively. F_2 crossovers from the vermilion, scarlet and oyster mutant males totalled 90 among the 1016 counted, 8.86 per cent.

Six of the seven androgenetic females were tested. Four of these produced 259 wild-type daughters, $\frac{pe\ \ pu}{+\ \ \ +}$, and 270 peach purple sons. They had mated with the wild-type males from the treated females. Offspring from 58 daughters of these androgenetic females showed peach-purple linkage as expected.

The fifth androgenetic peach purple female produced peach purple only, 26 females and 7 males. It is highly unlikely that this androgenetic female should have mated with an androgenetic male (only one was noted in the mass culture). A mating with a son of a treated female, wild-type but mosaic for a peach-purple deficiency, would have produced peach purple daughters, $\frac{pe\ \ pu}{-\ Df\ -}$. Thirteen were tested producing males only, many peach purple.

The sixth androgenetic peach purple female produced 68 wild-type and 6 pale peach, non-purple daughters and 41 peach purple sons. Fifteen of the wild-type daughters, $\frac{pe\ \ pu}{+\ \ \ +}$, were tested showing peach-purple linkage as expected. The six pale peach daughters were bred and proved to be peach-oyster compounds, $\frac{pe\ \ pu}{oy\ \ +}$. This androgenetic female had probably mated with a male mosaic for oyster, the son of an X-rayed female.

The two pale peach mutant females were compound for oyster mutations induced in the treated eggs. Purple linkage was shown in their progeny.

Four of the six scarlet mutant females tested showed purple linkage and normal viability of scarlet in their sons but the other two were scarlet-lethal producing no scarlet among their 109 sons. From their wild-type daughters scarlet-lethal females were derived, compound for peach and producing only peach sons. Linkage with purple was shown, totalling 463 parentals, 49 crossovers, 9.57 per cent. A scarlet lethal stock descended from one of these mutants was bred. Counts for eye color of offspring of scarlet mothers totalled females,- scarlet 1615, peach 1594 and males,- peach 4107, oyster mutant one.

The mutant female with dark red eyes, dahlia, proved to be dahlia-semilethal, *dasl*. Males with this gene are highly inviable and most of those that do mature are much deformed and separable for body color with difficulty. Sons of the mutant showed purple linkage of *dasl* giving an excess of peach

purple. The fifteen wild-type daughters tested included all four expected types,- 7 $\frac{pe\ \ pu}{+\ \ +}$, 1 $\frac{pe\ \ +}{+\ \ +}$, 1 $\frac{dasl\ \ pu}{+\ \ +}$ (which produced males,- wild type 66, purple 13), 6 $\frac{dasl\ \ +}{+\ \ +}$ (which produced females,- wild type 35, dahlia 25 and males,- wild type 467, dahlia 3.

Two of the 25 F_2 dahlia females produced males,- dahlia 35, dahlia purple 8, dahlia (purple?) 17, peach (mostly purple) 503, oyster purple mutant 1. Their $\frac{dasl\ \ +}{+\ \ +}$ mother had therefore mated with a peach purple brother.

Some of the dahlia males were relatively normal and it was possible to get matings with peach purple females. There resulted 321 dahlia females and 578 peach purple males. These dahlia females, $\frac{pe\ \ pu}{dasl\ \ +}$, produced males,- dahlia 91, dahlia purple 19, dahlia (purple?) 56, peach 143, peach purple 710. Males with dahlia eyes are far outnumbered by their peach-eyed brothers showing that the semilethal effect was still associated with the dahlia eye color. These relatively normal appearing dahlia males were therefore fluctuants of dahlia-semilethal rather than crossovers between dahlia and a closely linked semilethal.

Grandsons of selected relatively normal dahlia males were 166 dahlia, 853 peach, giving 19.46 per cent relative viability. In unselected stock there were 68 dahlia males with 1073 brothers, 6.34 per cent relative viability. The difference is very highly significant suggesting factors compensating for the semilethal influence of *dasl*.

Daughters of dahlia females crossed with their peach brothers total dahlia 168, peach 178, showing that the semilethal effect of *dasl* is recessive.

Crossovers between *dasl* and *pu* total 188, 17 per cent, among 1108 males that were separable for body color.

Mutants were found among the descendents of the androgenetic and mutant females of this experiment.

In addition to the deficiency suggested to explain the peach purple daughters of androgenetic female number 5 and the oyster found in six of the 74 daughters of androgenetic female number 6, there were ten unexpected eye-color types.

A mosaic female with a scarlet spot in her right eye, due either to a second mutation or to egg binuclearity, occurred among the wild-type daughters of one of the scarlet mutants. This mosaic female bred like her wild-type sisters, heterozygous for peach and purple. Among her sons were three oyster purple, spontaneous mutants probably from peach purple.

The six pale peach daughters of peach purple androgenetic female number 6 produced sons,- peach purple 297, oyster 259, peach 46, oyster purple 41 and daughters,- pale peach and peach purple many, peach and pale peach purple few, and a single scarlet purple. This spontaneous mutant bred as

compound for peach purple mated with a peach purple brother. The scarlet gene acted as a dominant to oyster- 250.6 and showed puprle linkage. The oyster- 250.6 stock was derived from a spontaneous *R*-locus mutant male.

Three oyster purple males occurred among the 14 peach and 92 peach purple sons of one of the scarlet-lethal mutants. One of these bred to scarlet-DR females proved recessive siring scarlet daughters which showed purple linkage in their offspring. The scarlet-DR stock was derived from the first X-ray *R*-locus scarlet mutation.

A peach purple female and a dahlia-semilethal female in F_2 from the dahlia-semilethal mutant female each produced a single oyster purple mutant male among their numerous peach purple sons. Each of these tested with scarlet-DR females proved recessive with purple linkage in F_2.

DISCUSSION

Dose-action curves have hitherto, for the most part, been based on lethals, either dominant or recessive. Lethals include a very great diversity of conditions cytogenetically, ranging from gross structural aberrations to submicroscopic alterations. Two-hit curves are expected from the former, one-hit from the latter.

It has generally been considered that rates for visible mutations should form a one-hit curve because visibles are regarded as point mutations. There is evidence that visibles affecting eye color induced in the eggs of Mormoniella by treatment with X-rays and with fast and slow neutrons do not form a one-hit curve but that the rate is increased disproportionately at higher doses (Kayhart, in press). The cytogenetic significance of this fact is not understood. These rates have been obtained by the first method mentioned in this paper, from counts of haploid males developed from treated eggs. Male haploidy has filtered out all lethals and the curves are based on survivors with all mutable eye color loci included.

Genetically considered, a "point" is a mendelizing unit which cytologically may be anything from an entire chromosome to a submicroscopic region of a chromonema. Points differ among themselves in mutability so that, while a curve based on many points may be repeated in different experiments, its cytogenetic significance is little if any better understandable than a curve for lethals.

A dose-action curve might be based on mutation rate at a single point, provided mutation frequency were high enough to make this possible. Data given in Experiment 1 of this paper indicate this to be the case for the *R*-locus of Mormoniella. Total rate for *R* alone is not statistically lower than rate for viables at all loci and unpublished data indicate that rate for viables at *R* actually exceeds rate for viables at all other loci taken together. This may be because the *R* locus is physically more extensive than other eye-color loci. Some of the compounds of *R* alleles exhibit complementarity, "pseudoallelism," and it is considered that there are two mutable color elements involved (Whiting, P. W., 1951, 1954). Rate for viables

at *R* cannot be directly determined from observation of males. Many tests of male mutants fail so that rate for *R* must be determined by extrapolation from the proportion of *R* mutants among those successfully tested.

The second method of collecting data for study of mutation rate should prove to be more satisfactory in that all visibles are recovered including those with recessive lethal effect. Moreover, the chance of establishing and maintaining a stock with each mutant gene is very high because most females will produce offspring. Thus it is possible not only to determine total rate at a single locus, but to identify almost every mutation with respect to its genotype as well as its phenotype. A phenotypically scarlet for example may be a viable, a recessive lethal or a female-sterile. It may affect one gene element or more than one. It may be a mutation from the wild-type allele or from any one of the mutant alleles. Scarlet mutants have already been obtained from several of these alleles, not only the colored but also oyster white.

Spontaneous mutations at the *R* locus occur with relatively high frequency in miscellaneous crosses involving different *R*-locus alleles. Their rate has not been determined because it was requisite to record only classes of offspring produced. For example, a mutant male crossed to a tester female, compound for two alleles, sires two types of daughters in equal numbers. A sample of each of these daughters produces two classes of sons in equal numbers. Establishment of the 1 : 1 ratio would be, in each case, both laborious and unneccessary. It can be observed at a glance that the types are at least approximately equal. Of more importance is the recording of the two colors produced. Then there may appear one or a few mutants quite distinct in color from their numerous sibs. These have in general proved to be in the *R* locus.

Data presented in this paper are but a small sample of those already obtained. It has become obvious that spontaneous rate in mixed pedigrees is higher than in pure stocks, although the former cannot be calculated because of incompleteness of counts. Studies are in progress in which pairs of stocks are being crossed and F_2 males counted. These already indicate significant differences among themselves and from rates for pure stocks. There is need for further testing of many different *R*-locus types to give a better understanding of this complicated series of genes.

SUMMARY

Induced mutations to bright eye colors in Mormoniella have hitherto been obtained by observation of sons of irradiated unmated females. Mutation rates up to one per cent of survivors thus obtained are based on viable changes at all eye-color loci. It has been shown by breeding tests of the mutant males that the majority of these mutations occur at a single locus called *R*.

The present paper presents a second method for securing mutations. X-rayed wild-type females are mated to untreated males with peach eyes, a

recessive at the *R* locus. Daughters produced are, therefore, wild-type unless a mutation has occurred at this locus. By this method mutation rate can be studied at a single locus and mutant types with recessive lethal effect are recovered as well as viables. It has been shown that, within the limits of the data, this total mutation rate at the single locus *R* is high being not significantly less than the rate for viables at all loci including *R*.

Androgenetic offspring, both males and females, are produced following irradiation of eggs.

In pedigrees following genetic tests of *R*-locus mutants, further mutations occur at this locus. Their rate has not been determined but it appears to be much higher than spontaneous rate in pure stocks.

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THE EFFECT OF OXYGEN CONCENTRATION ON THE DOSE-ACTION SURVIVAL CURVES OBTAINED FOR HABROBRACON EGGS IRRADIATED DURING MEIOTIC PROPHASE AND METAPHASE.*

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Thoday and Read (1947) found that bean root cells X-rayed in the absence of oxygen contained a lower proportion of chromosomal aberrations than those irradiated in the presence of oxygen. Later studies (Giles and Riley, 1949; Hayden and Smith, 1949; and Baker and Sgourakis, 1950) have shown that most types of genetic changes caused by X-rays vary with the oxygen concentration surrounding the cells at the time of irradiation.

Giles and Riley (1950) pointed out that the dependence of the genetic effects of X-rays upon oxygen concentration could be the result of an augmentation of the initial effect of the X-ray quanta or could result from inhibition by oxygen of the restitution of X-ray damage once it had occurred. They found that oxygen increased the percentage of aberrations only when present at the time of irradiation and had no effect before or after irradiation. From this they concluded that oxygen probably acted by augmenting the initial damage rather than by preventing restitution of damage.

Schwartz (1952) studied the effect of oxygen concentration on the production by X-rays of mosaic and non-mosaic phenotypes in corn. He assumed that a kernel mosaic for two closely linked markers was the result of a terminal deletion in the X-rayed pollen and considered a completely recessive kernel to be the result of an interstitial deletion in the X-rayed pollen. Irradiation in the absence of oxygen caused a greater percentage decrease in mosaic kernels than in recessive kernels, and Schwartz concluded from this that oxygen prevented the restitution of chromosomal damage in his material.

Whiting (1945a) found that X-rays cause a far higher percentage of lethality in Habrobracon eggs irradiated during meiotic metaphase-I than they cause in those eggs irradiated during meiotic prophase I with the same doses. Her cytological studies (1945b) showed that almost all lethality induced in prophase-I or metaphase 1 eggs resulted from the loss of parts of chromosomes during meiosis following irradiation. She suggested that meiotic metaphase eggs were considerably more sensitive to X-rays than

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meiotic prophase eggs because of a large difference in the ability of the chromosomes in each of these two stages to recover from X-ray damage. Metaphase chromosomes are stretched on the spindle and, according to her interpretation, X-ray damage probably results in the deletion of a terminal segment of the chromosome with little chance of restitution. In contrast to metaphase chromosomes, prophase chromosomes do not appear to be under tension and restitution of X-ray damage seems more probable.

On the basis of Whiting's findings, it seems likely that experiments with Habrobracon eggs can provide some information on the role of oxygen in augmenting the effects of X-ray damage to chromosomes. If oxygen prevents the restitution of chromosomal damage, oxygen concentration will have a very small effect on the percentage of lethality induced in metaphase eggs in which the restitution of chromosomal damage is relatively rare. On the other hand, prophase eggs irradiated in higher oxygen concentrations will show a higher percentage of lethality than those irradiated in the absence of oxygen because Whiting's data showing that prophase I eggs are relatively insensitive to X-rays indicate that damage to prophase chromosomes can be restored. A comparison of the effectiveness of oxygen in augmenting radiation damage in each of the two stages should provide evidence which supports the restitution hypothesis of Schwartz or the breakage hypothesis of Giles and Riley. This comparison has been made in the present study for various X-ray doses and the data obtained favor the breakage hypothesis.

In the series of experiments described below, the relationship of X-ray dosage to the induction of total lethals was determined in the presence of nitrogen, air, and oxygen. These lethality values were determined for unfertilized eggs of Habrobracon irradiated both in the prophase and metaphase of the first meiotic division. Simple techniques for studying the effects of X-rays on different meiotic stages have been worked out for this organism by Whiting (1945a).

EXPERIMENTAL RESULTS

Eggs in meiotic metaphase-I were irradiated with 396r, 1,120r, 1,493r, 1,862r, and 2,450r. At each of these dosages up to 1,862r, three groups of animals were irradiated in each experiment; one in nitrogen, one in air, and one in oxygen. Beyond 1,862r animals were X-rayed only in nitrogen because the results of the 1,862r experiment showed that 100 per cent lethality was induced in eggs X-rayed in air or oxygen above that dosage.

Results of the metaphase experiments are given in table 1. When irradiated in nitrogen the percentage of eggs hatching decreased progressively from 79.7 $\pm$4.0 per cent when irradiated with 396r to 8.0 $\pm$3.4 per cent of eggs irradiated with 2,450r. In air the percentage of eggs hatching at 396r was 49.2 $\pm$5.4 per cent and this dropped progressively until 0.2 $\pm$0.4 per cent were found to hatch at 1,862r. When irradiated in oxygen the percentage of eggs hatching was 40.6 $\pm$5.4 per cent at 396r and declined to 4.0 $\pm$

TABLE 1

HATCHING RATIOS OF HABROBRACON EGGS IRRADIATED IN NITROGEN, AIR AND OXYGEN DURING MEIOTIC METAPHASE I. FRACTIONS REPRESENT EGGS HATCHING OVER TOTAL EGGS COUNTED AND ARE SET EQUAL TO PERCENTAGE OF EGGS HATCHING PLUS OR MINUS 95% CONFIDENCE INTERVAL (2X STANDARD ERROR).

X-Ray Dosage in Roentgen Units	Metaphase I Irradiated in Nitrogen	Metaphase I Irradiated in Air	Metaphase I Irradiated in Oxygen
None	$\frac{139}{148} = 93.9 \pm 4.0\%$	....	$\frac{111}{117} = 94.9 \pm 4.0\%$
396r	$\frac{306}{384} = 79.7 \pm 4.0\%$	$\frac{162}{329} = 49.2 \pm 5.4\%$	$\frac{134}{330} = 40.6 \pm 5.4\%$
1120r	$\frac{260}{475} = 55.0 \pm 4.6\%$	$\frac{31}{479} = 6.5 \pm 2.2\%$	$\frac{11}{277} = 4.0 \pm 2.4\%$
1493r	$\frac{101}{320} = 31.6 \pm 5.2\%$	$\frac{7}{309} = 2.3 \pm 1.6\%$	$\frac{0}{99} = 0$
1862r	$\frac{91}{395} = 23.0 \pm 4.2\%$	$\frac{1}{443} = 0.2 \pm 0.4\%$	$\frac{0}{470} = 0$
2450r	$\frac{21}{262} = 8.0 \pm 3.4\%$	....	....

2.4 per cent at 1,120r and 0 per cent at 1,493r. The above studies were based upon a count of 4,570 eggs.

In the prophase experiments, eggs were treated with 2,100r, 8,050r, 14,000r, 21,000r, 26,600r, 32,200r, 37,800r, and 44,100r. As in metaphase experiments, three groups were irradiated at the same dose on the same morning in nitrogen, air, and oxygen with X-ray doses up to 32,200r. Eggs X-rayed with higher doses were irradiated only in nitrogen because none of the eggs receiving 32,200r in air or oxygen had hatched.

Results of these experiments, in which 4,846 eggs X-rayed during meiotic prophase were counted, are given in table 2. The percentages of eggs hatching of those irradiated in nitrogen during meiotic prophase decreased progressively from 91.7 ± 4.6 per cent of those given 2,100r to 25.9 ± 5.2 per cent of those given 44,100r. When irradiated in air, the percentages of eggs hatching decreased from 95.8 ± 2.8 per cent of those which received an X-ray dose of 2,100r to 8.3 ± 4.4 per cent of those which received an X-ray dose of 26,600r. No eggs hatched when irradiated in air with 32,200r. When X-rayed in oxygen during meiotic prophase the percentages of eggs hatching decreased from 91.9 ± 4.2 per cent when treated with 2,100r to 3.2 ± 2.6 per cent when treated with 26,600r. As in air, no eggs hatched when treated in oxygen with 32,200r.

The results given above for survival of eggs X-rayed in air agree in general with those of Whiting (1945a) although exact comparisons cannot be made in every case because many of her dosages were different from those used in the present study. The percentages of eggs hatching with each type of treatment are somewhat higher than those previously published by

TABLE 2

HATCHING RATIOS OF HABROBRACON EGGS X-RAYED IN NITROGEN, AIR AND OXYGEN DURING MEIOTIC PROPHASE I. FRACTIONS REPRESENT EGGS HATCHING OVER TOTAL EGGS COUNTED AND ARE SET EQUAL TO PERCENTAGE OF EGGS HATCHING PLUS OR MINUS 95% CONFIDENCE INTERVAL (2X STANDARD ERROR).

X-Ray Dosage in Roentgen Units	Prophase I Irradiated in Nitrogen	Prophase I Irradiated in Air	Prophase I Irradiated in Oxygen
2,100r	$\frac{133}{145} = 91.7 \pm 4.6\%$	$\frac{182}{190} = 95.8 \pm 2.8\%$	$\frac{160}{174} = 91.9 \pm 4.2\%$
8,050r	$\frac{279}{323} = 86.4 \pm 3.8\%$	$\frac{137}{197} = 69.5 \pm 7.0\%$	$\frac{164}{255} = 64.3 \pm 6.0\%$
14,000r	$\frac{167}{225} = 74.2 \pm 3.8\%$	$\frac{88}{211} = 41.7 \pm 7.0\%$	$\frac{55}{204} = 26.3 \pm 6.2\%$
21,000r	$\frac{173}{271} = 63.8 \pm 5.8\%$	$\frac{27}{228} = 11.8 \pm 4.2\%$	$\frac{18}{194} = 9.3 \pm 4.2\%$
26,600r	$\frac{68}{115} = 59.1 \pm 9.2\%$	$\frac{13}{157} = 8.3 \pm 4.4\%$	$\frac{7}{218} = 3.2 \pm 2.6\%$
32,200r	$\frac{119}{310} = 38.4 \pm 5.8\%$	$\frac{0}{286} = 0$	$\frac{0}{263} = 0$
37,800r	$\frac{130}{367} = 35.4 \pm 5.0\%$	....	....
44,100r	$\frac{74}{286} = 25.9 \pm 5.2\%$	....	....

the author (1954) for a similar series of experiments. The reason for this difference is explained by Dr. Anna R. Whiting's discovery that exposure of metaphase eggs to nitrogen for a long period of time can cause a decrease in the percentage of eggs hatching. Since all eggs treated in the nitrogen series of experiments previously reported were kept in nitrogen at least one-half hour, this nitrogen induced lethality was superimposed on the X-ray effects. The amount of lethality induced by nitrogen has been found by the present author to depend on more than one factor, and consistent data are most easily obtained by eliminating nitrogen induced lethality entirely. This can be done by keeping the exposure period of metaphase eggs under five minutes and it has been done in the experiments reported in table 1. Prophase eggs are either not affected by nitrogen injury or recover before they are laid.

Dose-action survival curves plotted for eggs treated during meiotic metaphase in nitrogen, air, and oxygen are shown in Figure 1 and similar survival curves for eggs irradiated in nitrogen, air, and oxygen during meiotic prophase are shown in Figure 2. The dose-action survival curves for eggs irradiated during meiotic prophase I and meiotic metaphase I in nitrogen and air are compared in Figure 3. The prophase and metaphase doses resulting in control survival in nitrogen (0r and 2000r) and 50% survival in nitrogen (1200r and 29,000r) have been superimposed in this figure. The

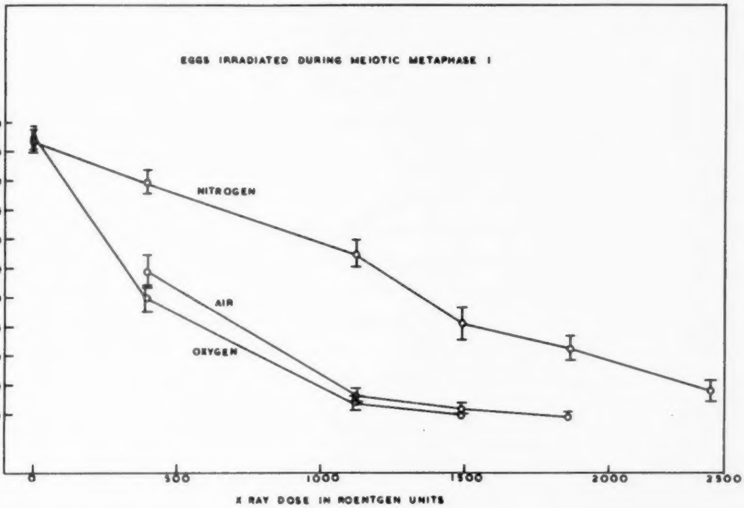

FIGURE 1. Dose-action survival curves for eggs irradiated during meiotic metaphase I. Bars represent 95% confidence intervals.

curves for irradiation in nitrogen do not differ significantly although 0% survival is reached at a lower comparable dose in prophase eggs than in metaphase eggs. This difference may reflect a difference in the type of damage causing lethality at higher doses as suggested by Whiting (1945a).

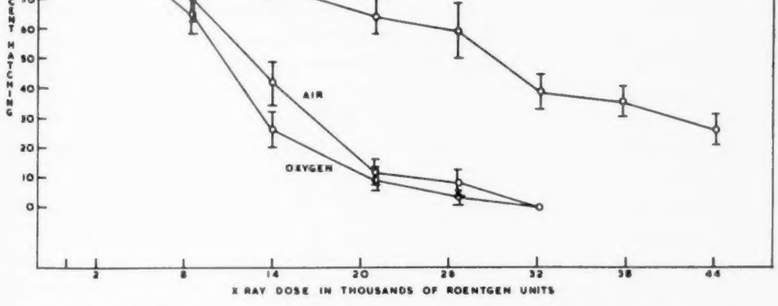

FIGURE 2. Dose-action survival curves for eggs irradiated during meiotic prophase I. Bars represent 95% confidence intervals.

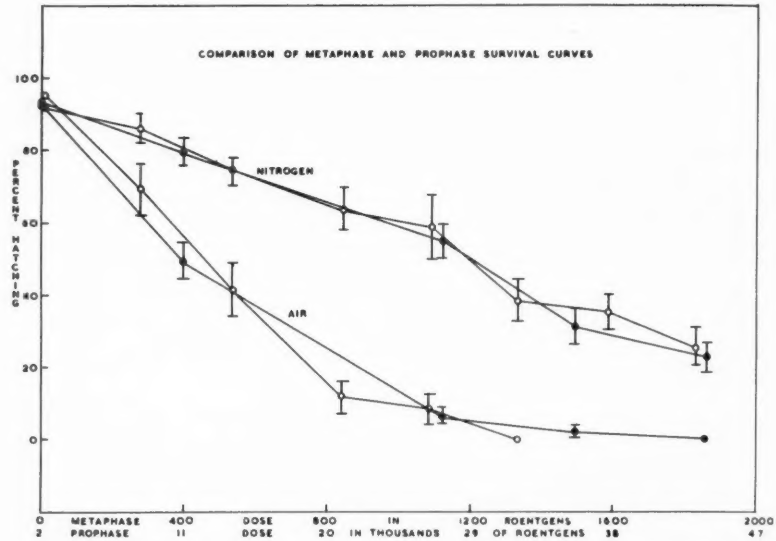

FIGURE 3. Dose-action survival curves for unfertilized eggs irradiated during meiotic prophase I and meiotic metaphase I in nitrogen and air plotted together for comparison. Solid black circles represent points for metaphase data; hollow circles represent points for prophase data. Bars represent 95% confidence intervals.

DISCUSSION

From the data presented above, it can be seen that the amount of lethality induced by a given X-ray dose is considerably lower when prophase or metaphase eggs are irradiated in nitrogen than when they are irradiated in air or oxygen. This difference increases rapidly with dose until a maximum difference is reached. In the case of metaphase eggs, the maximum difference was 48.5 per cent and in the case of prophase eggs the maximum difference was 52.0 per cent. If oxygen interferes with restitution, prophase and metaphase chromosomes must be capable of approximately the same amount of restitution. However, if this explanation is accepted, some explanation other than Whiting's tension hypothesis must be found for the extreme difference in sensitivity of the two meiotic stages. Since her tension hypothesis is well supported and fits all the data, it appears more logical to suppose that oxygen has its effect by being involved in the mechanism by which X-rays damage chromosomes rather than by interfering with restitution. The latter view is supported by cytological studies made by the author which will be published in detail elsewhere. In general terms, these cytological studies have shown that the proportion of terminal deletions and chromatin bridges present in eggs irradiated in nitrogen, air, and oxygen are the same as would be expected if these were the predominant sources of lethality. Further support has been provided by Whiting (1954) who found that all types of chromosome change (dominant lethals, reces-

sive lethals, and visible mutations) induced by X-rays in metaphase I eggs respond similarly to the absence of oxygen at the time of irradiation.

The author therefore interprets his data to support the views of Giles and Riley (1950) and Riley, Giles, and Beatty (1951) that oxygen increases X-ray damage to chromosomes by increasing the effectiveness of X-ray quanta in causing initial damage. The concept that oxygen augments X-ray damage by interfering with restitution of such damage as proposed by Schwartz (1952) does not seem to fit the data obtained in the present study.

Muller (1954) feels that Schwartz's data do not provide conclusive proof of the restitution hypothesis of oxygen action. He points out that the chromosomal structures causing mosaic and recessive phenotypes in Schwartz's material are unknown and such things as two-break rings or dicentrics may be involved in the mosaics.

SUMMARY

A comparison of the effect of oxygen in modifying lethality induced by X-rays in meiotic metaphase and in meiotic prophase Habrobracon eggs has been made. Since restitution of damaged chromosomes is considered to be rare in meiotic metaphase eggs and frequent in meiotic prophase eggs, the data obtained are of interest in deciding whether oxygen has a role in initial damage to chromosomes or in preventing restitution of damage.

Studies of total embryo lethals induced in 4,570 eggs X-rayed in nitrogen, air, and oxygen during meiotic metaphase with doses ranging from 396r to 2,450r were made. The nitrogen series differed very significantly from the air and oxygen series with a maximum difference of 48.5 per cent at one dose. Similar studies were made of 4,846 prophase eggs X-rayed in nitrogen, air, and oxygen with doses ranging from 2,100r to 44,100r. Again the nitrogen series differed significantly from the air and oxygen series with the maximum differences reaching 52.0 per cent at one dose.

The oxygen effect appears to be of the same magnitude in metaphase and prophase eggs despite a considerable difference in the X-ray dose necessary to induce lethality in each of these two stages. This similarity is believed by the author to support the initial damage hypothesis of oxygen action proposed by Giles and Riley (1950) and to be contrary to the expectations of the differential restitution hypothesis proposed by Schwartz (1952).

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DOMINANCE VERSUS OVER-DOMINANCE IN HETEROSIS: EVIDENCE FROM CROSSES BETWEEN OPEN-POLLINATED VARIETIES OF MAIZE*

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Arguments presented by Crow (1948 and 1952) demonstrated that if the dominance hypothesis, advanced by Jones (1917), for explanation of heterosis were correct the best hybrid that could be obtained using inbred lines extracted from an "equilibrium population" would excel that population by no more than the product of the number of effective loci and their average mutation rate. In this proposal an "equilibrium population" was referred to as one in which gene frequencies are at equilibrium between mutation and selection and genotype frequencies are those expected with random mating and independent assortment among loci. Assuming that 5000 and 10^{-5} are reasonable maxima for loci number and mean mutation rate, respectively, and that grain yield is equatable to fitness; a basis is provided for arriving at the five percent maximum superiority value for yield of a hybrid over a parent "equilibrium population." The sequence of Crow's argument, if applied to maize, then proceeds as follows:

(a) It is known that selected maize hybrids excel open-pollinated varieties in yield by much more than five percent.
(b) The dominance hypothesis fails as the explanation of heterosis.
(c) As an alternative to the dominance theory, overdominance (superiority of an heterozygous genotype over any homozygote at the locus level) is suggested as a plausible explanation.

The importance of overdominance in the explanation of gene action in maize had been advanced previously by East (1936) and Hull (1945).

The theoretical point made by Crow is relevant as a basis for inference from observations on relative performance of hybrids and open-pollinated varieties only if the latter are identical genetically, that is, in frequencies of all genes which affect yield. Differences in average grain yield between varieties and selected hybrids involving inbred lines from different varieties are not critical evidence relative to level of dominance unless the different varieties are all identical equilibrium populations. The normal procedure followed in making a double cross hybrid is to combine lines derived from different varieties. Results from Eckhardt and Bryan (1940) showed that highest yielding double crosses were obtained using single crosses of widely different parentage. If closely related lines are to be

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used in the same double cross hybrid, they are combined in the parental single crosses, insuring genetic divergency in the double cross.

The observation of heterosis in a cross of open-pollinated varieties constitutes unequivocal evidence of genetic difference between the varieties. The evidence for heterosis in yield in the majority of variety crosses was conclusive in the findings in investigations prior to 1920. Richey (1922) in a review of reports on variety crosses, noted that in 244 comparisons 82.4 percent of the crosses yielded more than the average of the parent varieties and 55.7 percent excelled either parent. If variety crosses exhibited heterosis 30 or 40 years ago, as seems established in the literature, there is little reason to doubt that heterosis would be obtained in crosses of present day varieties. Nevertheless, there is a possibility that selection in the varieties in the interim has brought them to a common equilibrium status.

As a part of a series of experiments designed to study genetic differences among varieties, six southern open-pollinated varieties were compared with the fifteen possible crosses among them. The six varieties consisted of three yellow-kernel varieties—Jarvis, Indian Chief and Simpson and three whites—Weekley, Biggs and Latham.

RESULTS

The crosses and parental varieties were compared in an experiment utilizing a randomized block design with five replications at three locations in 1952 and in 1953. Data were taken on yield of unshelled maize on ten equally competitive plants in each plot. The data for yield of parents and relative performance of crosses are given in table 1.

TABLE 1

YIELD OF OPEN-POLLINATED MAIZE VARIETIES IN BUSHELS (FIRST COLUMN), IN PERCENT OF THEIR MEAN (DIAGONAL), OF THEIR HYBRIDS IN PERCENT OF THE AVERAGE YIELD OF THE TWO PARENTS (ABOVE DIAGONAL), AND IN PERCENT OF THE HIGHER-YIELDING PARENT (BELOW DIAGONAL).

Varieties		Jarvis	Indian Chief	Weekley	Simpson	Biggs	Latham
	Yield (Bu./Acre)	Percent					
Jarvis	43.4	*110.7*	129.1	119.3	116.6	106.6	109.9
Indian Chief	38.0	(121.2)	*96.9*	127.5	124.1	132.2	146.2
Weekley	44.9	(117.3)	(117.8)	*114.5*	115.4	104.6	110.0
Simpson	40.4	(112.6)	(120.5)	(109.6)	*103.1*	109.2	125.0
Biggs	38.0	(100.0)	(132.2)	(96.6)	(106.1)	*96.9*	123.0
Latham	30.6	(93.7)	(131.9)	(92.5)	(109.8)	(111.0)	*78.1*
mean	39.2						

Standard error of the percentage difference between each cross and its mid-parent. (7.3%)
Mean of crosses relative to mid-parent. (119.9%)
Mean of crosses relative to high parent. (111.5%)

The yields of the parental varieties, given in the first column of table 1, exceed the average yield of all maize grown in North Carolina during the years of this study. In general, growing conditions encountered with the various tests were satisfactory considering that rainfall was below normal in 1952 and 1953 in most areas of the state.

The italicized diagonal values give the performance of each variety relative to the average yield of all varieties. The performance of the individual variety crosses, relative to the average of the two parental varieties and to the higher of the two parents is given in the upper right and lower left portions of the table, respectively. The standard error of the mean difference between the average of two parental varieties and their cross is 7.3 percent and is applicable to the percentage difference between each cross and its mid-parent.

DISCUSSION

The results reported here are in general agreement with the early work on variety crosses; namely that heterosis does occur. In this study crosses excelled mid-parents by approximately 20 percent and the higher parent by 11.5 percent. The heterosis observed, together with the variation between varieties, is clear evidence that these varieties are genetically different and therefore the difference between mean yield of varieties and yield of selected hybrids between lines from different varieties is not critical relative to level of dominance.

Crow's argument is most directly relevant to the comparative performance of a variety and hybrid obtained using only lines derived from that variety. Unfortunately few comparisons of this type are available in the literature due to the impractical nature of this procedure of combining lines to attain maximum yield performance. Such a comparison is available in the data reported by Eckhardt and Bryan (1940) where two double cross hybrids constituted from different arrangements of four inbred lines from the Black Yellow Dent variety were evaluated with the parental variety for three years. The average yield of hybrids was approximately 14 percent in excess of the variety; which, in the light of Crow's demonstration, suggests that heterosis in maize yield cannot be explained in terms of only complete or partial dominance. However, such data are still not critical unless it is established beyond reasonable doubt that the population from which the lines were derived is actually at equilibrium (i.e. cannot be improved by selection).

The established genetic divergencies of varieties raises these questions as to how varieties differ:

(a) Are the major varietal differences due to complete absence in one variety of favorable genes present in another? If so, each might or might not represent an "equilibrium population" with respect to its own segregating loci. Such quantitative differences in gene content could result either from inbreeding (finite population size) or from divergent mutational changes in non-interbreeding populations. If the varieties are partially in-

bred populations, which seems entirely plausible, then what is measured as heterosis in the hybrid vs variety comparison is in part "restoration of vigor lost by inbreeding" which can (see Crow, 1948 and 1952) be accounted for on the basis of simple dominance.

(b) Are these varieties at equilibrium at all? If not, progress in yield improvement should be possible in each through intra-population selection.

The genetic variability known to exist in varieties could be of the dominance sort produced by segregation at loci exhibiting overdominance which is essentially the explanation offered by Hull (1945) for failure of selection for higher yield to be effective in varieties. However, the small (less than 0.6) estimates of the ratio of dominance to additive genetic variance led Robinson, et al. (1955) to conclude that overdominant loci are not the single important source of genetic variability in yield in the Jarvis, Weekley and Indian Chief varieties. Preliminary results from selection studies in progress with these varieties indicate that yield improvement is being affected.

A practical implication of the observed heterosis in variety crosses is that selected pairs of varieties may prove desirable foundation material for use in reciprocal recurrent selection as proposed by Comstock et al. (1949). Since two varieties can be chosen that in their original state yield a cross for which performance approaches that of commercial double cross hybrids and in which the intra-variety genetic variance is considerable (Robinson et al., 1955) the prerequisites for desirable foundation stocks appear satisfied.

The heterosis and general agronomic appearance of crosses of varieties could provide the basis for choosing the source material for deriving inbred parents of superior hybrids. Variety cross heterosis should be indicative of the average performance of all hybrids from inter-variety crosses among the inbreds of the parental varieties but may not relate to the maximum possible hybrid performance from a specific combination.

The latter would excel the performance of the variety cross itself by an amount that is dependent upon, but that probably is not predictable in any simple manner from, the genetic variation within the varieties.

SUMMARY

Observation of heterosis in variety crosses of maize makes it clear that varieties are not genetically identical. Admitting genetic divergencies between varieties, any attempt to attribute the extent to which the heterosis is accountable in terms of complete dominance *or* overdominance is largely speculation when the criterion used requires identical gene frequency for all populations. The possibility of inbreeding is suggested to account for the genetic diversity between varieties and finally it is questioned whether any intra-variety gene frequency equilibria between mutation and selection have been reached in open-pollinated maize varieties.

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A MUTANT IN DROSOPHILA PSEUDOOBSCURA WHICH ALTERS THE PIGMENTATION OF THE TESTICULAR ENVELOPE WITHOUT CHANGING THAT OF THE EYES

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ORIGIN OF THE MUTANT

The mutant to be described in the present article has the property, unique among the known mutants in various species of Drosophila, in that it alters the pigmentation of the testicular envelope without at the same time affecting the coloration of the eyes of the fly. The more usual condition is that the pigment in the testicular envelope is absent or reduced in quantity in those mutants which show also a reduction of the amount of the red pigment in the compound eyes (see, for examples, the descriptions of the various mutants in *Drosophila melanogaster* in Bridges and Brehme, 1944).

The mutant, to be called *marbled* (symbol *mbl*), was found in November, 1954 in a culture of *D. pseudoobscura* derived from a wild female collected at Bryce National Park, Utah, in the summer of 1951 by Professor Th. Dobzhansky. In the normal flies, the red coloration of the testis can easily be seen through the abdominal wall from the ventral side; in the marbled mutant the abdomen seems to be devoid of the color. Dissection of marbled males showed the condition to be due to a mosaic discoloration of the testicular envelope, which is mostly colorless except for irregular-shaped splotches of the normal red pigmentation.

In the original culture only about 4 per cent of the males showed the marbled character. By back-crossing the daughters of marbled fathers to marbled males, 54 marbled and 110 normal males, together with 213 females, were obtained. Ten of the females were then crossed individually to marbled males. In three of the cultures all the sons were marbled, showing that the females as well as the males were pure for the gene *mbl*. A pure *mbl* stock was established from these cultures.

DESCRIPTION OF MARBLED

One hundred males from the marbled stock were dissected, and all of them showed a mosaicism in the testicular envelope, consisting of bright red and colorless areas. The patterns formed by the colored areas are quite irregular and variable from fly to fly; the colored areas are, however, indistinguishable in the intensity or the shade of the color from the pigmentation of normal testes. Only a single male had one of the testes wholly uncolored; the remaining flies had some coloration in both testes. The ex-

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tent of the colored areas varied from a single spot to more than half of the testicular envelope.

One hundred females from the marbled stock were dissected, and none of them showed any colored spots on the surface of the ovaries. Among 46 wild-type females, 11 had one or more red spots on the ovaries. These spots are usually very small but easily seen under a dissection microscope; most of them are elongated in shape, but some are star-shaped or branched. In no other organ was a difference in color detected between the wild-type and the marbled flies. In particular, the two classes of flies were found to possess exactly the same coloration of the eyes. The coloration of the Malpighian tubes is also identical.

The marbled gene nevertheless does produce a pleiotropic effect. About half of the flies of either sex in marbled cultures show an abnormal position of the wings in the resting state; namely, one of the wings is held out, its axis forming a right angle with the body, while the other wing is held in a normal position. Marbled flies showing this condition are unable to fly, and when disturbed jump some centimeters. This trait is recessive; it does not appear in heterozygous females.

Reciprocal crosses between the marbled and wild-type flies showed that *mbl* is a sex-linked gene. This was confirmed by tests with the marking genes Bare, orange, and Curly, located in the second, third and fourth chromosomes respectively. No linkage with *mbl* was observed.

ABSENCE OF EFFECT ON EYE COLOR

To exclude the possibility that the gene *mbl* may have an effect on the eye color too faint to be perceived, marbled flies were crossed to flies homozygous for orange and for orange and purple. The double and triple heterozygotes were examined, and were found to have eyes of normal color. Males were then obtained which carried the gene *mbl* in their X-chromosome, and were homozygous for orange or for orange-purple. No effects of marbled on the eye colors were observed. The marbled-orange males tended, however, to have fewer and smaller colored areas in the testicular envelope than is the case in the marbled non-orange males; namely, 10 out of 30 marbled-orange males examined had wholly colorless testes. This suggests an effect of the gene orange on the testis color in the presence of marbled, while orange by itself has no such effect. Yet, this hypothesis is not tenable, since when marbled was combined with orange from another stock the proportion of males with colorless testes has dropped. It seems that genes modifying the effects of *mbl* were present in the original orange stock, but that these modifiers are not related to the orange mutant as such.

CONCLUSIONS AND SUMMARY

The discoloration of the testicular envelope in the white-eyed mutant of *Drosophila melanogaster* was one of the first thoroughly studied instances of a pleiotropic effect of a gene mutation in Drosophila (see Dobzhansky,

1927, for citation of earlier literature). Since then, mutants which affect the color of the testes have been found in several species of Drosophila. All of these mutants influence, however, also the eye color, and are, in fact, detected originally as eye mutants. More particularly, the mutants which alter the color of the testicular envelope are those with eyes of the "brown" type, which have lost or diminished the amount of the red eye pigment. It is relevant to note that mosaic discoloration of the testicular envelope is a rule in mutants which induce also a mosaicism in the eye (Plum and others in *D. melanogaster*). Although relatively few eye-color genes are known in *D. pseudoobscura*, all the previously known ones in this species obeyed the general rule. The sex-linked gene marbled described above is an exception. It influences the distribution, though not the coloration, of the pigment in the testicular envelope. It has complete penetrance, though variable expressivity. Nevertheless, it appears to have no effect whatever on the coloration of the eyes. The developmental mechanisms which bring about this condition would be interesting to study.

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The author wishes to express his gratitude to Professor Th. Dobzhansky for his helpful discussions and suggestions concerning the present work, and for his aid in the preparation of the manuscript.

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Bridges, C. B. and Brehme, K. S., 1944. The mutants of *Drosophila melanogaster*. Carnegie Inst. Wash. Publ. 522: 1–257.

Dobzhansky, Th., 1927. Studies on manifold effects of certain genes in *Drosophila melanogaster*. Zeit. ind. Abst. Vererbungsl. 43: 330–388.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

CYTOTAXONOMY OF CURCULIONIDAE (COLEOPTERA)*

The weevil genus Hylobius Germ., erected in 1817, comprises the species *congener* D. S. and M., *pales* Boh., and *radicis* Buch. in North America. In Finland and Sweden it is represented by *abietis* L., *transversovittatus* Gze., *pinastri* Gyll., and *piceus* DeG. The last named species occurs also in North America, where Leconte, considering it generically distinct, transferred it to his new genus Hypomolyx in 1876.

The North American *Hypomolyx piceus* has been found by Warren (1955) to consist of two forms, one winged and the other almost wingless, which because of the presence of other correlated morphological differences led him to entertain the idea of their being specifically distinct.† It is apparently unknown whether the vestigial-winged one occurs in Scandinavia.

Since it had earlier been established that *Hylobius congener* possesses unusually well differentiated chromosomes (Smith, 1952), the possibility of establishing the taxonomic relationship of the normal- to the vestigial-winged *piceus* on the basis of chromosome number and/or morphology seemed especially promising, and, by extension, the soundness of Leconte's introduction of the name Hypomolyx appeared open to test.

Living adult males of *pales* and *radicis*, donated by the Forest Insect Survey, Sault Ste. Marie, in co-operation with associated Forest Insect Rangers; of *abietis* and *pinastri*, kindly air-mailed from Finland by Professor Dr. Esko Suomalainen of Helsinki University; and of the North American normal- and vestigial-winged *piceus*, courtesy of Mr. G. L. Warren; and, finally, slides of a normal *piceus* male, prepared by Professor Suomalainen, make up the material briefly reported on here.

In agreement with the constitution already established for *congener*, *Hylobius pales*, *radicis*, *pinastri*, and *abietis* were each found to have 2n = 22 chromosomes: 10 pairs of autosomes and an Xy sex-determining mechanism in which the y is relatively minute and associates with the X to form a parachute ("Xy_p"; Smith, 1950). The normal-winged form of *piceus*, both from North America and Finland, is profoundly different in that it has 2n = 40 chromosomes: 19 pairs of autosomes showing little di-

*Contribution No. 257, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

†This has recently been confirmed by Wood (unpub.).

versity in size and a typical Xy_p sex-determining mechanism. The vestigial-winged *piceus* is intermediate. It has 15 pairs of autosomes along with an X chromosome and possibly a much smaller y that, if present, is at the limit of resolution of the microscope. The autosomes, however, instead of falling into a graded series of moderate size, as they do in the normal-winged form, include two pairs that are extremely large, perhaps as much as four times the size of the remaining ones. The differences between the chromosome complements of the two forms are thus of sufficient magnitude to establish them as distinct species, one having been derived through a series of autosomal "fusions" or the other through one of autosomal fragmentation. Since "centric fusion" (White, 1954) of non-homologous chromosomes is the simpler process and since populations of another weevil have recently been encountered that comprise homozygous "fused," homozygous "unfused," and heterozygous "fused" individuals (unpub. data), the vestigial-winged form is logically regarded as being the derivative species.

On the other hand, the numerical uniformity of the chromosome complements of the North American and Finnish species of Hylobius (*sensu* Leconte)—there are morphological differences characterizing the chromosome sets of some, at least, of the species—and their marked difference from *piceus* clearly validate the separation of Hypomolyx from Hylobius.

The nicety of this cytological cleavage has recently been thrown open to question by a chromosome survey of curculionids published by Takenouchi (1955). This author has established the following counts: *Hylobius albosparsus* Boheman, 2n = 40; *Hylobius galloisi* Kôno, 2n = 36; *Hylobius exsculptus* Roelofs, 2n = 28; and *Hylobius montanus* Kôno, 2n = 20. Perhaps the first two will actually prove to be species of Hypomolyx, with *Hylobius galloisi* representing one of the expected "fusion" types intermediate between 2n = 40 and 2n = 32. Unfortunately Takenouchi's illustrations are in insufficient detail and at too low a magnification to allow comparative analysis, so that the significance of his findings remains at present obscure.

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Smith, S. G., 1950, The cytotaxonomy of Coleoptera. Canad. Entom. 82: 58–68.

1952, The cytology of *Sitophilus* (*Calandra*) *oryzae* (L), *S. granaria* (L.), and some other Rhynchophora. Cytologia 17: 50–70.

Takenouchi, Y., 1955, A chromosome survey in thirty species of the weevils (Curculionidae, Coleoptera). Jap. J. Zool. 11: 425–441.

Warren, G. L., 1955, Root injury to conifers in Canada by species of *Hylobius* and *Hypomolyx* (Coleoptera: Curculionidae). Forestry Chron. (in press).

White, M. J. D., 1954, Animal cytology and evolution. The University Press, Cambridge. 454 pp.

STANLEY G. SMITH

FOREST INSECT LABORATORY
SAULT STE. MARIE
ONTARIO
November 4, 1955

THE AMERICAN SOCIETY OF NATURALISTS

Secretary's Report, 1955

The annual business meeting of the Society was held in East Lansing, Michigan, on the Campus of Michigan State University in connection with the AIBS on the evening of September 7th, 1955, with President K. V. Thimann presiding. A motion was made and unanimously passed to hold the next annual meeting with the AIBS in September, 1956, at Storrs, Connecticut.

The report of the Nominating Committee (Ernst Mayr, chairman, Bentley Glass, and Alfred E. Mirsky) was presented by the Secretary. With no further nominations from the floor the following officers were unanimously elected: President for 1956, E. Newton Harvey, Princeton University; Vice President for 1956, Frank A. Brown, Jr., Northwestern University; Secretary for 1956–1958, Bruce Wallace, Biological Laboratory, Cold Spring Harbor, N.Y.

Forty-six persons, nominated by members and approved by the Executive Committee, were elected to membership. Names of those accepting membership will be included in the roster of members to be published in the next issue of the Records. Six of the ten Honorary Members, Warder C. Allee, Charles E. Allen, Liberty Hyde Bailey, Albert F. Blakeslee, George H. Parker, and George H. Shull, died in the past year. On recommendation of the Executive Committee the following persons were elected to Honorary Membership: Benjamin Duggar, Richard Goldschmidt, J. T. Patterson, Fernandus Payne, Franklin Shull and Sewall Wright.

The reports of the Treasurer, C. P. Swanson; of the Auditing Committee, R. F. Kimball, Chairman; and of the Secretary, W. P. Spencer, were read and approved. The Society voted to approve the adoption of the Revised Constitution of the AIBS. A revision of By-law 3 of the Constitution of the Naturalists was adopted unanimously. The revised by-law reads as follows: "The Executive Committee shall be empowered to appoint an Editor for *The American Naturalist*, to serve for a five year term. The Executive Committee, in consultation with the Editor, shall appoint an Editorial Board to advise the Editor in matters of policy. Each member of the Editorial Board shall serve for a term of three years."

The Annual Report of L. C. Dunn, Editor of *The American Naturalist*, was read and approved.

A motion of thanks to the officers of the AIBS, to Michigan State University, and to Allen Fox, local representative of the Society, was passed.

At a meeting of the Executive Committee, with six of the seven members in attendance, L. C. Dunn was reappointed Editor of *The American Naturalist* for a five year term, beginning January 1st, 1956. The Executive Committee appointed the following individuals to serve as members of the Edi-

torial Board for the three year period from January 1st, 1956, to December 31st, 1958: W. Frank Blair, M. Demerec, Libbie H. Hyman, D. D. Keck.

On invitation from the Genetics Society of America and by unanimous vote of the Executive Committee the Naturalists have undertaken to serve as cosponsor of the Tenth International Congress of Genetics, to be held in Montreal, Canada, August 20-27, 1958.

At the East Lansing Meeting on the evening of September 7th, K. V. Thimann gave his Presidential Address on the subject: "Promotion and Inhibition; Twin Themes of Physiology," a comprehensive survey of the field of plant hormones. Vice President Butler presided and introduced the speaker. On Thursday afternoon a symposium on "Modern Approaches to Problems of Differentiation," arranged by Vice President Butler, was presented. Subjects and speakers were:

Intracellular Differentiation, Tracy M. Sonneborn

A Consideration of the Determination of Tissue Cells, John P. Trinkaus

Physiological Processes Involved in the Conversion of Normal Plant Cells to Tumor Cells, Armin C. Braun

Internal Factors Controlling Cell Differentiation in Flowering Plants, William P. Jacobs

On Wednesday the Society cosponsored a symposium on "The Taxonomy of Cultivated Plants" dedicated to L. H. Bailey. On Thursday morning the Society cosponsored a symposium on "Quantification in Population Ecology." At the meeting of the AAAS, in Atlanta, Georgia, on December 28th, 1955, the Society served as cosponsor of a symposium on "The Species Problem," arranged by Ernst Mayr.

The Executive Committee of the Naturalists for the year 1956 consists of E. Newton Harvey, Chairman, Frank A. Brown, E. G. Butler, M. Demerec, W. P. Spencer, C. P. Swanson, K. V. Thimann, and Bruce Wallace. Representatives on the AAAS Council for 1956 are S. G. Stephens and one other to be appointed. The Representative on the AIBS Governing Board for 1956 is C. G. Huff.

During the past year the following deaths have occurred: E. B. Babcock, H. B. Bigelow, A. H. Hersh, Carl Moore, R. C. Osburn and F. D. Richey, in addition to those already mentioned above. The year 1955 closed with an active membership of approximately 480.

Attention is again called to the fact that on retirement from professional service an active member may become emeritus, with exemption of annual dues. Emeritus members may continue to subscribe to *The American Naturalist* for the $3.50 subscription rate paid by the Society for each active member. Request for emeritus status should be sent to the Secretary and subscription fee should be sent to the Treasurer, C. P. Swanson, Johns Hopkins University, Department of Biology.

At the end of a three year term of office perhaps a few observations are in order. It is not surprising that a biological organization, established in 1883, by a small group of American naturalists for the purpose of "dis-

cussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution etc.," should itself have undergone some evolution in the interim.

At the present time the Society serves three functions:

(a) as an Honorary Society in which election to membership serves as recognition of sustained research activity of a high order;

(b) as an organization for arranging and sponsoring Symposia of breadth and wide interest;

(c) as a group which controls the editorial policy of *The American Naturalist*, but does not own the journal.

Do these objectives justify the continuance of the Society? They do if the present membership, and that means each individual, will do his share toward their proper attainment. Many of you know individuals in your own or other departments who have, over a period of years, carried on a sustained research program and turned out publications of high merit, and are worthy of election to membership. If our present membership will take this matter seriously the organization can serve more effectively as a healthy stimulus to young biologists. Members wishing to make nominations should send a vita together with a bibliography, which need not be complete, but which should contain important recent publications, to the Secretary.

Furthermore there is another responsibility which comes with acceptance of membership in an organization such as the Naturalists. If you continue to achieve in your field do not resign your membership on the ground that the Society no longer has anything to offer you. Perhaps you have something to offer the Society and through it to those younger men who may benefit by the stimulus which a little recognition brings. Those of us who see the resignation lists, not large but too large, wonder sometimes why certain individuals feel that they can no longer afford to do their share toward maintaining the organization which provided for them this same stimulus, earlier in their research careers.

Perhaps you may never be asked to participate in a symposium. But you could make it a point to attend those arranged. You might even send constructive suggestions to the officers on the type of symposia which you and others would favor. It would, of course, be possible for the Society to expand its program in this field. However, examination of either the AIBS or AAAS programs indicates that there is already a plethora of symposia at these meetings. Any expansion here should look toward the setting up of regional meetings apart from these organizations.

Concerning the third objective it may be said that *The American Naturalist*, under the able Editorship of Dr. Dunn, is a journal of which we may be proud. With a strong Editorial Board representing a variety of biological disciplines, not under the domination of any one school of thought, the journal should continue to improve. As a member you may help the quality of the journal by submitting papers which contribute to biological synthesis

in these days of rather narrow specialization, and by calling attention of potential contributors, who need not be members of the Society, to this medium for publication.

In conclusion your Secretary takes this opportunity to thank all those, both officers and members, who have cooperated in the work of the Society in this three year period.

Respectfully submitted,
WARREN P. SPENCER
Secretary

REPORT OF TREASURER

August 15, 1955

AMERICAN SOCIETY OF NATURALISTS

Balance, November 16, 1954	$ 939.38
Income from dues: Nov. 17, 1954, to Aug. 15, 1955	2,598.00
Total receipts	$3,537.38
Expenditures: Nov. 17, 1954, to Aug. 15, 1955	
Stamps	18.00
AIBS membership	249.50
L. C. Dunn, editorial assistance	300.00
Science Press, 496 subscriptions to *American Naturalist*	1,736.00
Realart Press, envelopes	11.00
A. F. Carr, overpayment of dues	1.50
Bank handling charges	4.51
Total expenditures	$2,320.51
Balance, First National Bank, Baltimore, Aug. 15, 1955	$1,216.87

C. P. SWANSON
Treasurer

REPORT OF THE EDITOR—1955

This report covers the period Jan. 1—Aug. 31, 1955, because of the date of the annual meeting. In this period 62 mss were considered of which 41 were published, 2 rejected, 1 withdrawn and 18 held over. The published material includes 32 articles, 7 letters to the editors, 2 book reviews and 20 pages of book notices.

The contents of the 1955 volume show a change in the direction of the desired increase in diversity of fields covered. Genetics still leads, largely because one issue was devoted to the symposium of the Genetics Society, but there were several papers on ecological, natural history and general evolutionary problems. Data papers declined in number, those with emphasis on synthesis increased, in accordance with editorial policy.

L. C. DUNN

PUBLICATIONS RECEIVED

No undertaking to publish reviews is implied in acknowledgement of publications received. Books for notice may be sent to:

EDITORIAL OFFICE, The American Naturalist
Box 2, Schermerhorn Hall, Columbia University
New York 27, N. Y.

Berrill, N. J., 1955. The origin of vertebrates. 257 p., ill. $4.00. Oxford University Press, New York.

Comar, C. L., 1955. Radioisotopes in biology and agriculture. 481 p., ill. $9.00. McGraw-Hill Book Company, Inc., New York.

Darwin, Charles, 1955. The expression of the emotions in man and animals. 372 p., ill. $6.00. Philosophical Library, New York.

Reprinted with introduction by Margaret Mead and added new illustrations of animals and men.

Demerec, M. (Editor), 1955. Advances in genetics, Vol. VII. 309 p. $7.50. Academic Press, Inc., New York.

The seventh volume of this annual publication contains the following articles: Vernon Bryson and Waclaw Szybalski, Microbial drug resistance; Adriano Buzzati-Traverso, The 'Obscura group' of the genus Drosophila; A. Brito da Cunha, Chromosomal polymorphism in the Diptera; John A. Moore, Abnormal combinations of nuclear and cytoplasmic systems in frogs and toads; Paul B. Sawin, Recent genetics of the domestic rabbit; Ryuhei Takahashi, The origin and evolution of cultivated barley.

Dice, Lee R., 1955. Man's nature and nature's man. 329 p. $5.00. University of Michigan Press, Ann Arbor.

Ekblad, Martin, 1955. Induced abortion on psychiatric grounds. 238 p. Ejnar Munksgaard, Copenhagen.

Franklin, T. Bedford, 1955. Climates in miniature. 137 p., ill. $3.75. Philosophical Library, New York.

Gray, Peter, 1954. The microtomist's formulary and guide. 794 p., ill. $10.50. McGraw-Hill Book Company, Inc., New York.

Illingworth, Frank, 1955. Highway to the north. 293 p., ill. $7.50. Philosophical Library, New York.

Imms, A. D., 1951 (reissue). Insect natural history. 317 p., ill. $5.00. McGraw-Hill Book Company, Inc., New York.

Wardlaw, C. W., 1955. Embryogenesis in plants. ix + 381 pp., ill. $7.00. Methuen & Co., London; John Wiley & Co., New York.

Professor Wardlaw discusses and illustrates embryological development in all classes of plants, and he considers to what extent visible embryonic development might be interpreted in terms of genetical, physiological, physical, and environmental factors. He is particularly interested in demonstrating how the study of plant embryology may further knowledge of plant morphogenesis, and how it may help to clarify problems of phylogeny, homologies of organization, parallel and convergent development. By way of introduction it is shown that morphogenetic principles and factors, such as genic and chemical control of development, polarity, cell division, segmentation patterns, gradients of cell size, spatial relationships, and the phenomenon of the organism as a reaction system, command attention in embryogenesis, and an experimental approach is suggested. There follow twelve chapters in which Dr. Wardlaw presents both the general morphological features and points of specific interest for Algae, Bryophyta, Psilotales and Equisetales, Lycopodineae, Eusporangiate Ferns, Leptosporangiate Ferns, Gymnosperms, and Flowering Plants. The last-named group comprises three chapters; the first deals with general features and embryonic types; the second with particular aspects, e.g., embryogenesis in primitive and advanced angiosperms, origin of the monocotyledonous embryo, parasites and saprophytes, apomixis, polyembryony; the third with analytical and experimental investigations, including embryo culture and ovular tumors. The general theme of the introductory chapters is taken up again in the final part which gives a summary of the general morphological features of embryos as well as a list of morphogenetic factors and discussion of protoplasmic organization. The bearing of embryogenesis on questions of phylogeney is also discussed here, and it is stated that "the factors which determine the embryonic development must be much more fully explored before embryological data can be used with safety in taxonomy and phylogeny."

There can be little doubt that in the past many students have been discouraged from working with the ordinarily small and rather inaccessible embryos of plants. Progress in experimental and chemical respect has therefore remained relatively small. It is Dr. Wardlaw's contention that technical difficulties may be overcome, and that general botanical problems may be considerably advanced through experimental work with plant embryos. Knowledge of the inception of embryonic patterns and of early formative processes may yet bring about better understanding of adult organization, it may also lead to a fresh outlook on the taxonomic and phylogenetic significance of morphological features.

There are numerous line drawings, text references, an extensive bibliography, and a general index.

ROBERT BLOCH